REPRODUCTIVE BIOLOGY OF FEMALE FISHERS
IN SOUTHCENTRAL MAINE

By Thomas F. Paragi

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An Abstract of the Thesis Presented in
Partial Fulfillment of the Requirements for the
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The reproductive biology of 12 radio-collared female fishers (Martes pennanti) ≥2-yrs-old (adult) was studied from February 1984 to December 1989 in a 600 km^2 study area in southcentral Maine. Twelve adult females were monitored, 7 for ≥1 year, for 25 fisher-seasons (season = March-June). Estimated whelping dates (n = 12 litters) were 3 March-1 April (median = 21 March, interquartile range = 14-29 March). Use of natal dens typically began during mid-late March and ended during early June. Kits generally stayed within the mother's home range until being trapped in November (1 male) or dispersing in January (2 females). Intensive monitoring during 1988-89 caused females to move kits more often than during 1986-87, but no kits were abandoned.

All natal dens occurred in tree cavities (n = 33). Hardwoods composed 94% of the dens examined, 1986-89, with aspens (Populus spp.) accounting for 52% of all den trees.

Annual rate of natal denning by adult females averaged

60% (range 0-100%). Five litters in natal dens averaged 2.0-2.2 kits per female, 1988-89. Survival rate of kits from ca. 6 weeks until late October was a minimum of 0.6. Estimated rate of fall recruitment was 0.7-1.3 kits per female, substantially less than ovulation rate (3.0 ova per female $\geq$1 yr).

Proportion of adult females with placental scars (75%, _n_ = 20 fisher carcasses from central Maine, 1988-89) more closely corresponded to annual denning rates (60%) than did occurrence of blastocysts in carcasses of females $\geq$1-yr-old (85%, _n_ = 41), suggesting that implantation rate is less than ovulation or fertilization rates. Teats on female fishers that suckled young (_n_ = 7) were larger than those on a female that had not suckled young, suggesting that the proportion of adults with enlarged teats could be an annual index to the proportion of females raising young.

Average annual survival rate [95% CL] was 0.69 [0.54,0.88] for females $\geq$1 yr and 0.19 [0.08,0.47] for juveniles of both sexes. Average annual fall recruitment needed to maintain the population (2.1 kits per female) was greater than the observed rate (0.7-1.3), suggesting a population decline. Annual estimates of population increment (λ) were <1.0 except when annual survival of females $\geq$1 yr was 1.0 in 1986. Catch per unit effort for September-October livetrapping (1985-89) and catch rates of successful trappers (1977-88) were consistent with the estimated population decline. The fisher harvest in southcentral Maine should be reduced to allow population recovery.

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A THESIS

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This work is dedicated to my mother, who did not live to see it completed. Any accomplishment of mine is ultimately hers.

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I. INTRODUCTION

Harvest Management in Maine

Fishers (Martes pennanti) have been an economically important furbearer in Maine since the 1800s, and trappers still pursued them even when fishers became scarce in the early years of this century (Coulter 1960). By the 1930s, the species was restricted to the remote, heavily-forested region of northwestern Maine. Except for a trial open season in 1950, trapping for fishers was prohibited in Maine from 1937-54, during which the population grew and expanded its range south and east. Regulated harvesting began in 1955, and today the fisher inhabits most of the state (Clark 1986).

The average price of fisher pelts increased from ca. $40 in the early 1970s to ca. $120 by the early 1980s (Clark 1986). Fishers continue to have the most valuable pelt of furbearers in Maine, with females worth 1.5-2.0 times more than males (MDIFW, unpubl. data). As fur prices increased during the 1970s, so did exchange of information on trapping techniques, fur handling, and marketing (de Almeida and Cook 1987). Trappers wishing to pursue fishers were better equipped, more mobile, and potentially more effective than trappers in the past.

Fishers are susceptible to traps set for other terrestrial furbearers; therefore, it is impractical to

(Coulter 1960, 1966; Powell 1982). The MDIFW has primarily controlled the harvest of fishers since 1976 by having a single open season for terrestrial furbearers, with season length and opening date set in part to limit the fisher harvest (Clark 1986). Southcentral Maine supported the highest harvest density of fishers, averaging 6.6/100 km^2 from 1978-82 and 4.1/100 km^2 from 1983-88 (Clark 1986; MDIFW unpubl. data). In 1984, southcentral and southern Maine had the highest trapper density (5.4/100 km^2) (Clark 1986).

Data for managing fisher harvests in Maine typically are collected from past harvests. Beginning in 1973, the MDIFW instituted mandatory tagging of the pelts of several furbearers, including fishers, to estimate harvest density, total harvest, and harvest per successful trapper (Clark 1986). During 1950-64 and 1978-84, the MDIFW collected fisher carcasses from trappers and cooperated with universities to examine the indices of age and sex of the harvest (MDIFW unpubl. data), body condition (Rego 1984), and reproduction (Coulter 1960, 1966; Shea et al. 1985).

Background and Purpose

In 1980 the MDIFW identified a need to estimate population densities of fishers and to predict the effects of habitat change and harvest on fisher populations (MDIFW 1980). A study began in 1983 in southcentral Maine to address these needs (Arthur 1988, Arthur et al. 1989_a_, 1989_b_, Arthur and Krohn 1990). Annual denning rates for

~~1989b, Arthur and Krohn 1990)~~. Annual denning rates for adult females (≥2 yrs) ranged from 0%-75% during 1984-87 (~~Krohn et al~~. 1990). Although these rates were based on small samples ($\underline{n}$ ≥ 5 females), they were much lower than reported ovulation rates of 95-97% (Shea et al. 1985, Douglas and Strickland 1987). Because the occurrence and mean number of corpora lutea have been suggested as reproductive indices and for use in population models (Shea et al. 1985, Douglas and Strickland 1987), there is concern that allowable harvest based on ovulation rates may overestimate per capita litter size of fishers (Arthur and Krohn 1990). Also, there is little data on litter size, neonatal mortality, the denning period, and postweaning biology of fishers (Powell 1982, Leonard 1986). This study was conducted from February 1988 to December 1989 to further quantify reproductive rates and examine aspects of denning biology in wild fishers.

Study Area

The study area encompassed ca. 600 km^2 centered around Brooks and Monroe in Waldo County, Maine (44°30'N, 69°05' W; Fig. 1); it was described in detail by Vonk (1975) and Arthur et al. (1989a, 1989b). This coastal region consisted of rolling hills to 370 m covered primarily by mixed forests interspersed with small farms and pastures, including farmland reverting to forest. Temperature ranged from a mean low of -9 C in January to a mean high of 20 C in July,

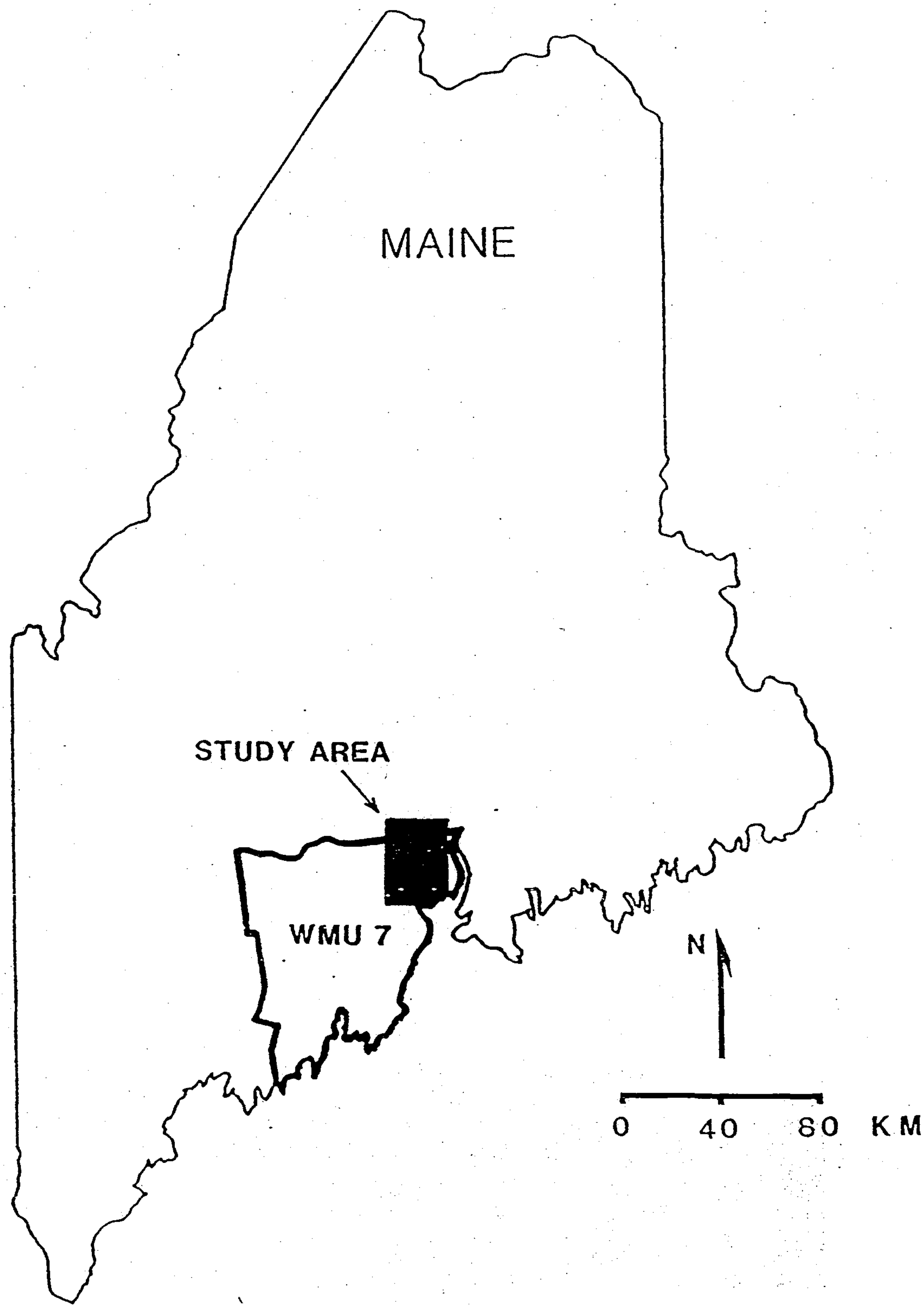


Fig. 1. Location of study area for the fisher project in Waldo County, Maine, 1984-89. Wildlife Management Unit (WMU) 7 is an administrative region of the MDIFW.

and annual precipitation was ca. 90 cm (U.S. Weather Bureau 1982).

Human density in the core towns of the study area (Brooks, Jackson, Monroe, and Swanville) was $10.3/km^2$ in 1987, an increase of 53% since 1970 (Welch 1983, 1989). For comparison, the human density in Waldo County was $16.2/km^2$ in 1987, an increase of 32% during the same interval. The area of agricultural land in Waldo County has declined by 76% since 1920 but only by 14% since 1969 (U.S. Bureau of Census 1920, 1969, 1987). A network of paved and unpaved secondary roads, some of the latter not maintained, occurred throughout the study area, so few points were >1 km from a road. Hardwood (deciduous) and softwood (coniferous) trees were harvested for firewood, pulp, and timber on primarily private land.

II. NATAL DENNING AND POSTWEANING BIOLOGY OF FISHERS IN SOUTHCENTRAL MAINE

Direct observations on the reproductive biology of wild fishers are rare because fishers exist at low density in forested habitat and adults are solitary outside of the breeding season (Coulter 1966, Powell 1982). Most data on neonatal fishers are from litters raised on fur farms in Canada (Hodgson 1937, Hall 1942). Coulter (1966) and Powell (1982) also described the development of a litter from a wild female in captivity. Seton (1909), Grinnel et al. (1937), and Hamilton and Cook (1955) provided anecdotal accounts of natal denning, litter sizes, and family behavior in the wild.

The development of radiotelemetry allowed individual females to be followed throughout the reproductive cycle. Kelly (1977) first used telemetry to describe the movements of an adult female with kits. Leonard (1980, 1986) monitored an adult female for 2 years and described her movements, activity patterns, and attentiveness to a natal den. Arthur and Krohn (1990) described activity patterns of 14 denning and nondenning females during spring and summer and provided data on den trees and the denning period. My objectives were to (1) describe the duration of the denning period and types of natal dens used by adult females with kits, (2) compare activity patterns among individual females with kits during denning, and (3) describe spatial relationships of mothers and their kits before kits disperse.

METHODS

Fishers were captured and fitted with radio collars (model S2B5, Telonics, Inc., Mesa, AZ) during March 1984-December 1989 according to procedures described by Arthur (1988), except that in 1989 the transmitter collars included a leather insert that would decay and separate if the animals were not recovered (cf. Hellgren et al. 1988). A first premolar was removed, and one person prepared all teeth and interpreted cementum annuli using procedures of (Strickland et al. 1982).

Radio-collared fishers were located using 2-element Yagi antennas from small aircraft or by triangulation on the ground (Arthur et al. 1989a) at least once per week. Locations were plotted on 1:24,000-scale topographic maps (U.S. Geological Survey, Washington, D.C.) using universal transverse mercator coordinates. Accuracy of aerial and ground triangulation for 1984-87 were ≤150 m and ≤10 m, respectively (Arthur et al. 1989b). Accuracy of ground triangulation in 1988-89 was assessed by confirming the locations of females resting at natal dens following triangulation, where den locations were known to within 100

m. Antennas were hand-held during triangulation in 1988, but were mounted on a wooden rack atop a pickup truck in 1989.

Denning Period

I attempted to locate adult females daily from late February to mid June to determine if they consistently rested in the same hollow trees, presumed by Arthur and Krohn (1990) to be natal dens. Location of these dens was verified by quietly approaching and circling the den to confirm the source of the transmitter signal. Denning was estimated to have started on the first day that $\geq$3 consecutive triangulations were $\leq$100 m from a later-confirmed den; dens were typically visited on the third day that triangulations indicated a similar location. I assume kits were born when the initial den was established. Dens were then visited every 2-4 days, and establishment of subsequent dens was noted. Natal denning ended when the female stopped using any single resting site for more than 2 consecutive days. Ancillary to field work, dates of whelping by captive fishers were obtained from one fur farmer each in Massachusetts and New York.

Natal Den Characteristics

Most trees used as natal dens during 1986-89 were revisited by project personnel for closer examination after denning ended. Dens were characterized by tree species and condition (alive, partly dead, or dead). Slope, aspect, overstory, and understory of surrounding forest (hardwood, softwood, or mixed; Arthur et al. 1989a) were noted. Height and dbh of tree and height and size of cavity entrance were estimated in 1986 and 1987. Four trees in 1988-89 were unsafe, but most trees were climbed by project personnel, and the following were measured: dbh, height of cavity entrance, entrance size, cavity diameter and depth, and cavity aspect. The scope of data collection expanded after 1987, so all characteristics were not estimated or measured during 1984-86. Cavity openings were tested for an equal distribution of aspect using Rayleigh's test (Zar 1984:443).

Den Attentiveness and Kit Observations

Attentiveness of one female to a natal den was monitored in 1986, 1988, and 1989. In 1986, a Telonics TR-2 receiver was used, and maximum signal strength during a 15-min period was recorded by a CR21 Micrologger (Campbell Scientific, Inc., Logan, UT). In 1988-89, signal strength was recorded continuously using an AVM Falcon V receiver (Custom Electronics of Urbana, Inc., Urbana, IL) and a Rustrak model 288 stripchart recorder (Gultan Industries, Manchester, NH) (Licht et al. 1989). Instruments were powered by a 12-V motorcycle battery and secured in a waterproof box ca. 75 m from the den. A shielded coaxial cable (RG-58U) was connected to the antenna jack on the receiver, and the opposite end was lashed to a tree ≤3 m from the den, at a height similar to the cavity entrance.

Approximately 45 cm of the shielding was removed from the end of the cable near the den to act as an antenna. Sensitivity of the system was adjusted using the gain control so that a signal was recorded only when the female was ≤15 m from the antenna (i.e., in or near the den); this was tested using a spare transmitter. Instruments were checked daily. During the first two or three visits, I circled the den with a receiver to verify presence or absence of the female, but I rarely approached the den on subsequent visits. The recording system remained for a day or two after females moved the kits before it was moved to a new den. In 1989, I stopped monitoring a female in late April because she seemed to move dens more frequently than expected from past data on denning.

In 1988 and 1989, den cavities were searched when the female was temporarily absent to verify the presence of offspring 6-8 weeks after the initial den was first used. I did not attempt earlier visits for fear of delaying return by the mother during the cold, damp weather in early spring. Kits were sexed, weighed, measured for total length, and fitted with ear tags (Appendix A). Mothers and kits were periodically observed after denning (mid June-early August) by quietly approaching when the mother's transmitter signals were steady, indicating a resting animal.

Activity Patterns of Adult Females

The activity patterns of four adult females with kits were monitored from 31 March to 28 June 1988 using the strength and consistency of the radio signal to classify the fisher as active or resting (Kelly 1977). The circadian cycle was divided into four periods: dawn (2 hour s prior to sunrise - sunrise), day (09:00-15:00), dusk (sunset - 2 hours after sunset), and night (21:00-03:00 or between dawn and dusk); sunrise and sunset times were determined by averaging times for Augusta and Old Town, Maine (U.S. Naval Observatory, Nautical Almanac). Activity sampling was proportional to length of period, with dawn and dusk sampled once per week and day and night sampled three times per week. Each female was monitored for all periods during the 12 weeks; thus, distribution of activity samples was the same for all females. The order in which females were sampled within a period was changed each sampling bout. Sampling was by triangulation, and each of three or more bearings obtained within 30 min was monitored for a minimum of 2 min to discern signal integrity (cf. Lindzey and Meslow 1977:415). Although monitoring based on signal integrity might be a poor representation of specific activities (Garshelis et al. 1982), it may provide a reliable estimate of general patterns of activity (Lindzey and Meslow 1977). Arthur and Krohn (1990) assumed that bias in activity classification of fishers was consistent across time of day and season; I also assumed that activity bias was consistent among individuals to assess relative differences in activity among females.

Sampling of circadian periods was separated by ≥12 hours. Sampling periods for activity of females with kits were separated by ≥12 hours. Arthur and Krohn (1990) determined that there was no significant relationship between probabilities of being active on 2 consecutive locations separated by ≥2 hours. From sessions of continuous monitoring, Arthur (1987) found fishers tended to be active for periods of 1-6 h, separated by resting periods of similar length. Because heavy rain or wind >25 km/hour hindered telemetry procedures and interpretation of signal integrity, sampling was rescheduled if either occurred during monitoring.

I divided the 12 weeks of activity sampling into the periods of preweaning (30 Mar-14 May) and postweaning (15 May-28 Jun) based on kit development (see **Discussion**) and their end of dependence on milk at 8-10 weeks of age (Coulter 1966, Powell 1982). Main effects and interactions of individual females, circadian periods, and weaning periods on activity were tested simultaneously using an analysis of repeated counts (Koch et al. 1977) with marginals as the response (CATMOD procedure; SAS, Inc. 1985). In separate analyses, I tested for difference in proportion of diurnal locations classified as active for two females monitored during 1988-89 using a z-test (Zar 1984:396).

Spatial Relationships of Mothers and Kits

Spatial relationships of mother-kit pairs were examined from August 1988 to January 1989. The home ranges of adult females were delineated using a minimum convex polygon of telemetry locations from the postweaning period (early June 1988 to late January 1989); >60 independent locations (separated by ≥16 h) were used (Arthur et al. 1989b) except for an adult female that was killed in late August (n = 38 locations). Locations during June were daily and occurred throughout the circadian period, whereas most locations after June were diurnal every 3-5 days. For any female, no independent location was >1.3 km from any other, so I did not exclude any locations as outliers from the home range. Core areas of activity for adult females were defined by harmonic mean isopleths using 50% of the independent locations (Dixon and Chapman 1980). All ranges were produced using the microcomputer program MCPAAL (M. Stuwe and C.E. Blohowiak, Conservation Research Center, National Zoological Park, Smithsonian Institute, Front Royal, VA), with 10 grid intersections used for the harmonic mean isopleths. One kit from each litter in 1988 was captured and radiocollared in the home range of its mother between August and October 1988. Locations of kits between capture date and loss of radio contact, death, or dispersal (>8 km movements from the natal area) were overlaid on the respective home ranges and core areas of their mothers.

The movements of mothers and their kits in relation to each other were tested for attraction or avoidance during 1988 using a variation of nearest-neighbor analysis (Major and Sherburne 1987; Litvaitis and Harrison 1989). Separation distances between paired locations of a mother and kit were measured on scaled maps. All paired locations were obtained by triangulation within 1 hour of each other, and locations of each individual were separated by ≥16 hours (i.e., independent with respect to movements; Arthur et al. 1989b); however, actual locations were not confirmed. The frequency distribution of observed separation distances was compared to an expected distribution generated from randomly selected locations of mothers and kits.

RESULTS

Twelve adult (≥2 yr) female fishers were monitored during 1984-89 for a total of 25 fisher-seasons (season = Mar-Jun denning period). Median telemetry error using a hand-held antenna for 32 triangulations in 1988 was 175 m; 75% of errors were ≤325 m. In 1989, median error on 17 den triangulations using the rooftop antenna was 100 m; 75% of errors were ≤150 m. Distance from transmitter to receiver usually was ≤1.5 km for both years, and personnel using telemetry equipment were unaware of accuracy testing.

Denning and Whelping Periods

Natal denning typically began in mid-late March and ended in early June (Fig. 2). Estimated whelping dates for the 12 litters in Waldo County were 3 March-1 April (median = 21 March, interquartile range [25th-75th percentiles] = 14-29 March). Physical and behavioral development of wild kits (Appendix A) corresponded closely to development of known-age kits raised in captivity (Coulter 1966, Powell 1982). Whelping dates for wild-bred females on fur farms in Massachusetts and New York ($\underline{n}$ = 19) and two captive litters in Maine (Coulter 1966:74) ranged from 26 February-6 April (median = 14, interquartile range = 2-16 March).

Females used 1-5 different cavities during the denning period (Fig. 3). Dens were used a median of 22 days (range 2-90, $\underline{n}$ = 33). Median straight-line distance moved by females relocating their kits to new natal dens was 575 m (range = 150-2650, $\underline{n}$ = 21). Females crossed paved or maintained dirt roads on only 1 of 21 occasions while moving kits to a new den. However, the crossing occurrence for 4 females with kits while traveling during the denning seasons in 1988 and 1989 (15 of 100 randomly-chosen pairs of independent, consecutive locations) was not different from the crossing occurrence while moving kits ($\underline{z}$ corrected for continuity = 0.91, $\underline{P}$ = 0.38).

Natal Den Characteristics

All natal dens occurred in tree cavities. Hardwoods

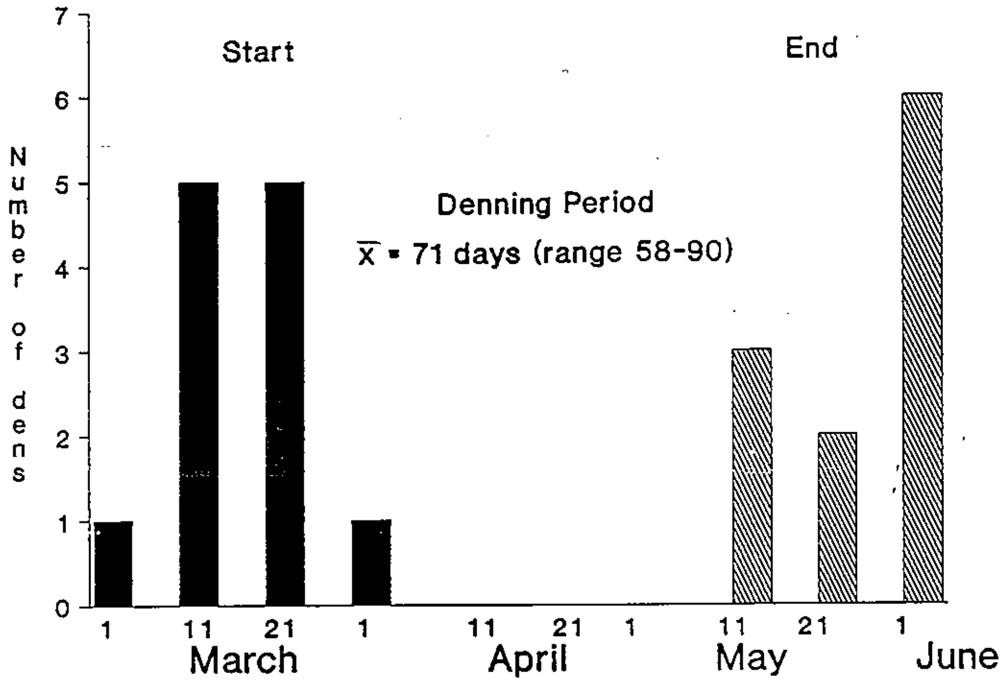


Fig. 2. Starting and ending dates for natal denning by 8 female fishers (3 monitored >1 yr) in Waldo County, Maine, 1986-89 (one female slipped her radio collar during denning).

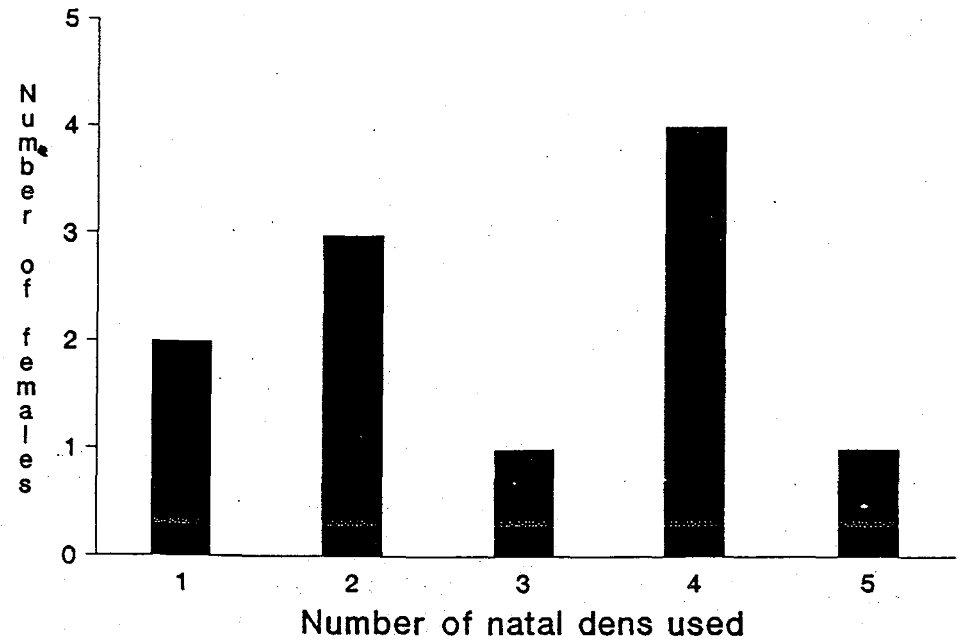


Fig. 3. Frequency of number of natal dens used by 7 adult females (3 monitored >1 yr) in Waldo County, Maine, 1986-89.

composed 94% of 33 den trees examined, with aspen (Populus spp.) accounting for 52% of all dens (Table 1, Appendix B). Initial dens (n = 12) were not different from subsequent dens (n = 20) for dbh, height and size of cavity entrance, or cavity volume (Mann-Whitney U, P >0.36). Fifteen (50%) of 30 den trees were dead, 9 (30%) were partly dead, and 6 (20%) were alive. Cavity aspect of 18 dens was not uniformly distributed (Z = 3.004, P = 0.048), and the mean angle (171°) was toward south. Eleven (73%) of 15 den sites had no terrain aspect (were flat). Overstory occurrence for 32 dens was 56% hardwoods, 25% mixed, and 19% softwood, with various types of understory vegetation. No prey remains were observed inside cavities or adjacent to den trees. Similar to the use of natal dens, 85% of 33 tree cavities used as resting sites by female fishers during 1984-89 were in hardwoods (cf. Table 1), including ash (Fraxinus sp.).

Den Attentiveness and Kit Observations

Monitoring of den attentiveness is summarized in Table 2. The proportion of each day that a female spent at a den in 1988, based on days with uninterrupted (24 hour) monitoring, declined during the denning period (r_s = -0.571, n = 35, P < 0.0005, 1-tailed). This female was presumed to be resting (based on signal integrity) on 42% of 24 independent locations known to be away from the natal dens; several were ≤0.5 km from a den. Females briefly visited former dens periodically after the kits had been moved to a

Table 1. Characteristics of natal dens in trees used by fishers in Waldo County, Maine, 1986-89. Dbh (cm), height (m) and area (cm_2) of cavity entrance, and cavity vc (m^3) were not different between aspens and other hardwoods (Mann-Whitney U; *P* >0.20).

	Tree dbh			Entrance height			Entrance area[a]			
Tree type	Med.[b]	IQR[c]	*n*	Med.	IQR	*n*	Med.	IQR	*n*	% Dead
Aspens[d]	45	38-45	17	7.0	5.0-10.0	17	78	63-95	14	63
Other Hardwoods[e]	60	45-75	13	5.1	4.4-7.5	10	108	85-149	8	36
Softwoods[f]	43		2	9.9		2	520		1	0
All Dens	45	39-60	32	6.3	4.6-9.0	29	95	70-110	23	48
Range	25-92 cm			0.9-12 m			140-1570 cm^2			

[a]Area of entrance = (pi x length x width)/4.

[b]Median.

[c]Interquartile range.

[d]Balsam poplar (*Populus balsamifera*) and bigtooth aspen (*P. grandidentata*).

[e]Red maple (*Acer rubrum*), sugar maple (*A. saccharum*), yellow birch (*Betula alleghaniensis*), red oak (*Quercus rubra*), American basswood (*Tilia americana*), and American elm (*Ulmus americana*).

[f]Northern white pine (*Pinus strobus*) and Eastern hemlock (*Tsuga canadensis*).

Table 2. Attentiveness of female fishers to natal dens as measured continuously by a stripchart recorder. Plots of continuous monitoring are in Appendices C, D, and E.

Female	Dates monitored	No. dens	Days[a]	% of time at dens[b]
F459	1-10 April 1986	1	8	54
F401	4 April-9 June 1988	3	35	45
F460	18 March-24 April 1989	3	6	57

[a]Entire 24 hours (00:00-23:59) uninterrupted by equipment failure or female moving the den.

[b]Mean percentage of uninterrupted days that a female was ≥15 m from the den.

new den or after natal denning had ended. Ten kits from 5 litters were handled in 1988-89 (Appendix A). Kits inside the den were silent when the mother was absent; in her presence, mewing was occasionally heard (cf. Leonard, 1986:38). In 4 of 5 instances, adult females moved the kits to another natal den by the day after handling of kits; one female moved the kits 2 days after handling. No litters were abandoned.

Ten observations (10-20 min each) of mothers and kits in trees and on the ground during mid summer suggested that kits had not yet developed the agility and balance of adults (cf. Coulter, 1966; Powell, 1982). Offspring were seen inside tree cavities with the mother on five occasions; kits 11 weeks old were observed to struggle when climbing, lose their grip, fall to the base of the cavity, and engage in raucous squabbles with litter mates. One 14-week-old kit that was resting on branches in close proximity to its mother awkwardly ascended a tree for a short distance when I approached; it then climbed down the tree, evidently curious, when I stopped near the base of the tree. Adult females typically watched observers, occasionally moving a short distance if they were resting on tree limbs; often they did not seem alarmed. Food habits of fisher families are in Appendix F.

Activity Patterns of Adult Females

Activity patterns were influenced by individual variation among adult females and by the interaction of female and circadian period (Table 3). For example, F401 had a much smaller proportion of active locations (0.21, n = 19) at night after weaning than did the other females (0.59-0.68, n = 17-19). An interaction of circadian and weaning periods also occurred; it was most evident at dawn, when the order of increasing proportion of active locations among the four females was reversed from preweaning to postweaning. Multiple comparisons among females (Zar 1984:401-402) using proportion of locations when female was active (all sampling periods combined) confirmed that the female with 3 kits was more active than those with 1-2 kits, but age and experience also must be considered in the comparisons (Table 4). Snow cover during activity sampling was patchy, persisting beneath coniferous overstory until late April.

The proportion of diurnal locations when F401 was active from 1 March-15 May was not different (P > 0.50) between 1988 when she had two kits (0.19, n = 53) and 1989 when she had none (0.29, n = 42). Likewise, the proportions were not different (P > 0.50) from 1 March-30 June for F460 between 1988 when she had 1-2 kits (0.25, n = 79) and 1989 when she had 3 kits (0.26, n = 78). Individual variation among females may affect activity levels more strongly than the annual variation in litter size in a particular female.

Spatial Relationships of Mothers and Kits

Prior to being trapped in early November (1 male) or

Table 3. Analysis of repeated counts (CATMOD procedure; SAS Inc., 1985) on activity of 4 female fishers with kits. Female, circadian period (dawn, day, dusk, night), and weaning period (prewean, postwean) are main effects, with activity as the response.

Effect	*d.f.*	X^2	*P*
Female	3	12.54	0.0057
Circadian Period	3	3.34	0.3425
Weaning Period	1	1.23	0.2672
Female * Circadian	9	22.86	0.0065
Female * Weaning	3	2.44	0.4866
Circadian * Weaning	3	9.39	0.0245
Fem. * Circad. * Wean.	9	9.86	0.3621

Table 4. Comparison of activity (Apr-Jun), litter size, and age among 4 adult female fishers. Proportion of active locations was significantly different (pairwise differences, *q* distribution; *P* < 0.0001) for 5 of 6 comparisons but not for F460 vs. F414 (*P* > 0.50) (e.g., Zar 1984:402).

Female:	325	460	414	401
Proportion of active locations (*n*):	0.63 (82)[a]	0.48 (100)	0.46 (100)	0.33 (101)
Age (yrs):	6	3	4	7
Litter size:	3	1-2	1	2

[a]F325 slipped her collar and was not monitored for 1.5 weeks in April-May until captured and recollared.

dispersing in late January (2 females), kits generally were located within the minimum convex polygons representing the home ranges of their mothers (Fig. 4). Prior to the death of F414 in late August (illegally shot), her kit (M391) was often located near previously occupied natal dens. M391 was located throughout most of F414's range after her death. M391's collar stopped transmitting in January 1989, but he was livetrapped in March 1989 on the edge of his mother's home range.

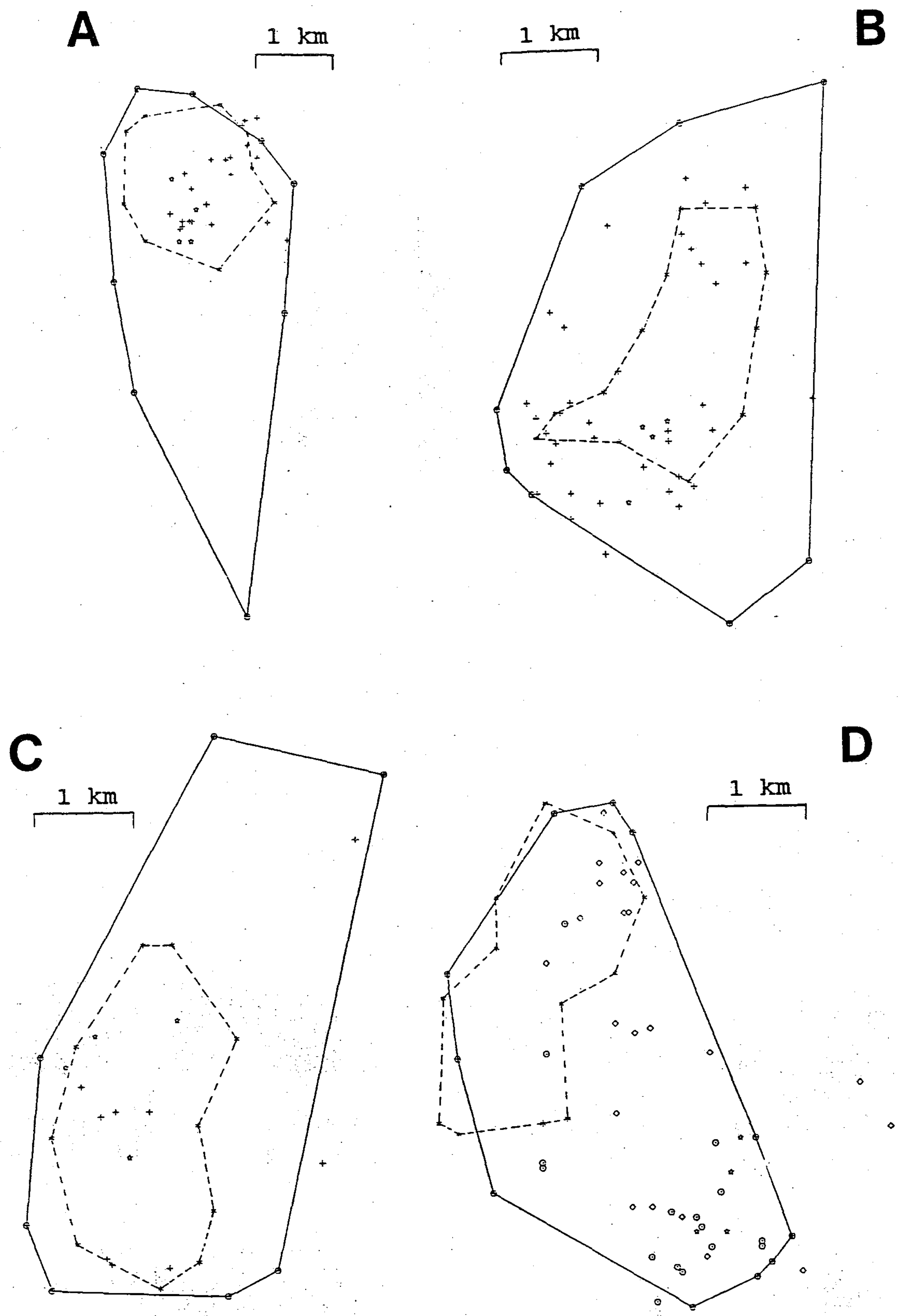
Sixty-eight percent of the paired locations ($\underline{n}$ = 62) of mothers and kits were $\leq$15 min apart. Analysis of separation distance showed no significant attraction or avoidance (Fig. 5). Seven pairs of triangulations, in August and September, were $\leq$350 m apart. Given median telemetry error in 1988, these fishers could have been together. The last observation of a mother and kit together was for a male kit seen in a tree with his mother on 10 August.

DISCUSSION

Denning Biology

The timing and duration of denning and number of dens used by fishers seems consistent with prior studies. Most whelping in wild fishers occurs in the latter half of March. Although whelping by captive fishers can occur in late

Fig. 4. Spatial relationships of adult female fishers and their offspring in Waldo Co., Maine, 1988-89. Minimum convex polygons of postdenning home ranges of adult females (AF) are delineated with solid lines, and harmonic mean models (50% isopleth) of core areas are delineated with dashed lines. All locations of juveniles (J) are plotted as '+,' except JM391 is plotted as '⊙' before his mother's death and '◇' after. Natal dens are plotted as '☆.' A: AF401 (n = 67 locations, 2 Jun - 20 Jan); JF211 (14 Oct - 20 Jan, dispersed). B: AF460 (n = 65, 2 Jun - 20 Jan); JF200 (9 Sep - 20 Jan, dispersed). C: AF325 (n = 61, 2 Jun - 29 Dec); JM206 (5 Oct - 12 Nov, trapped). D: AF414 (n = 38, 2 Jun - 22 Aug, killed); JM391 (10 Aug - 14 Jan, transmitter failed).


A
1 km
1 km
B
C
1 km
D
1 km

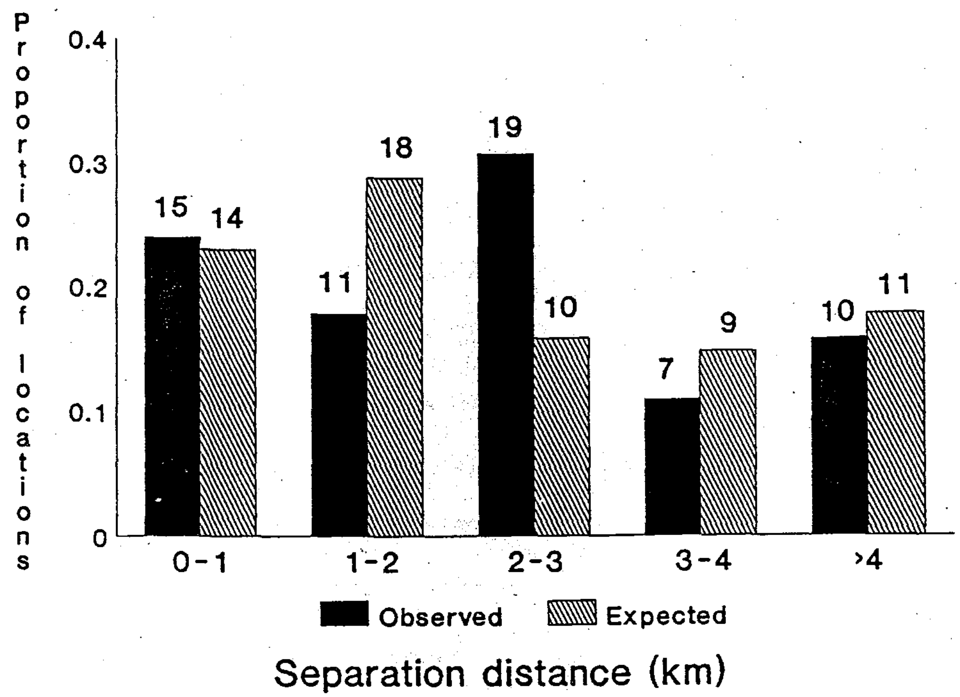


Fig. 5. Separation distances for 4 pairs of mothers and kits in 1988, based on 62 simultaneous locations between August 1988 and January 1989 (predispersal). There was no significant attraction or avoidance ($\underline{X}^2$ = 6.25, 4 d.f., P = 0.18). Randomly paired locations of mothers and kits were selected from actual data. Sample sizes are above bars.

February (unpubl. data from New York) to mid April (Hall 1942), most whelping dates for fishers in the northeastern U.S.A. occurred during the first half of March. Perhaps conditions of captivity (e.g., food, temperature, light, reduced energy expenditure) cause earlier implantation of blastocysts than in the wild.

Leonard (1980:94) noted that a female fisher in Manitoba whelped ca. 1-3 April and remained at a single den with kits until 27 May. Duration of denning for 2 litters in Connecticut (22 Mar-9 Jun and 30 Mar-12 Jun; P. W. Rego, Conn. Dept. Environ. Protect., pers. commun.) was similar to Maine litters, and both Connecticut females used two dens. Females in Maine ($\underline{n}$ = 6 fisher-seasons) used 1-3 dens during 1986-87, whereas during 1988-89 females ($\underline{n}$ = 5 fisher-seasons) used 4-5 dens. Also, all dens used <16 days ($\underline{n}$ = 10) and 88% of dens used <22 days ($\underline{n}$ = 14) were in 1988-89. This suggests that the more intensive monitoring I did on the latter group (den attentiveness, handling kits) may have caused females to move kits to new dens more frequently. End of denning was similar for Connecticut and Maine.

Females might be unwilling to move their kits across frequently-used roads during natal denning. A female carrying young may be hindered in running and climbing and might be more susceptible to vehicle mortality (see Chapter 4) or harassment by domestic dogs (Canis familiaris). Thus, an increasing density of paved or maintained dirt roads in the study area might effectively reduce the amount of denning habitat.

Tree Cavities

Leonard (1980:141-142) suggested biological advantages of elevated den cavities compared to ground dens for raising altricial offspring, including warmer air temperature, protection from infanticide by male fishers (if females select a small cavity entrance), and protection from ground-dwelling predators. In 92% of 25 trees where entrances were visible, cavity entrances were in the bole, reducing the "view factor" to the sky and heat loss by radiation (Thorkelson and Maxwell 1974:37-38). Cavity entrances tended to face south, presumably to increase capture of solar radiation and reduce wind exposure.

Most natal dens used by fishers in this study and mentioned in the literature were in hardwood cavities, primarily aspens. Aspens are susceptible to cavity formation via heart rot early in life (Boyce 1961), are highly susceptible to fungal infection (Meinecke 1929), and experience vertical decay at almost twice the rate of other northern hardwoods infected with common heart rots (Silverborg 1959). Four den trees in Connecticut (bigtooth aspen, Eastern hemlock, hickory [Carya sp.], and maple) had traits similar to dens in Maine, except the cavity entrance in the hickory was ca. 20 m above the ground (P. W. Rego, pers. commun.).

Den Attentiveness

As the denning period progresses, the proportion of each day that is spent at or near the den likely reflects the changing needs of mothers and kits. At the start of denning, the mother must often be present for warmth and to lick the anogenital region of kits to stimulate defecation and urination (Ewer 1968:252-253). As kits grow and their pelage develops, they can better thermoregulate when their mother is absent; this allows the mother to spend more time hunting or resting away from disturbances of the kits. Also, natal dens may become too warm for the mother. One female was observed to salivate for >15 min while resting at the entrance of a natal den in late May (S. M. Arthur, pers. commun.).

Activity Patterns of Adult Females

Variation in activity among adult females is likely caused by different energetic needs corresponding to litter size, age of female, and experience. Also, females may develop a pattern of hunting or resting during a part of the circadian cycle. One female showed no difference in activity during the denning period between 1988 (2 kits) and 1989 (no kits); however, Arthur and Krohn (1990) found that a denning female was more active during daylight hours in March-August than nondenning females (n = 7). Because of individual variation, activity patterns of fishers should be characterized based on data from several animals.

Spatial Relationships of Mothers and Kits

Arthur (1987) suggested that radio-collared juveniles were independent of radio-collared adult females by late September. Coulter (1966) observed that a female in captivity became hostile toward her two 4-month-old kits (mid-late July), killing one and injuring the other at 5.5 months. This suggests an innate social avoidance initiated by the adult, although the confines of a pen may have exacerbated the response observed by Coulter. Bekoff (1989) suggested that young carnivores may remain dependent on care-givers for food and protection even after they can negotiate their environment and make brief forays, especially when developmental information such as complex hunting skills can be gained (e.g., safe and successful kill of porcupines [Erethizon dorsatum]: Coulter 1966, Powell 1982). Because young fishers are relatively altricial and must develop specialized hunting skills, some may not be fully independent of the mother until late autumn if hunting skills are learned from the mother. I observed no overt avoidance within the mother's home range; perhaps dispersal is initiated by the kits in some instances. Brief observations of wild kits suggest that males are more aggressive than females (Appendix A), and dimorphism in body size is evident by early fall, with males becoming larger (Coulter 1966, Powell 1982). Perhaps variability in the degree of independence and observed dates of kit dispersal

(S. M. Arthur, pers. commun.; Paragi, unpubl. data) reflect not only sex-specific physical and behavioral development of kits but variation in tolerance by adult females.

III. ESTIMATES OF FISHER RECRUITMENT AND SURVIVAL: IMPLICATIONS FOR MANAGEMENT

Caughley (1977:1) described population dynamics as the difference between birth and death rates. Estimating per capita litter size (kits per all adult females) at birth is difficult in wild animals, so biologists frequently estimate recruitment rate, which is per capita litter size diminished by mortality of offspring to some time postpartum. Although this recruitment rate is not equal to the birth rate of a population, it provides a means to estimate population growth if the death rate is known.

Birth rate in fishers has been estimated from litter sizes of captive animals (Hodgson 1937, Hall 1942, Coulter 1966, Powell 1982, Leonard 1986), ovulation rate as measured by counts of corpora lutea (Eadie and Hamilton 1958, Wright and Coulter 1967, Kelly 1977, Shea et al. 1985, Leonard 1986, Douglas and Strickland 1987, Kuehn 1989), and fertilization rate as measured by counts of blastocysts (Hamilton and Cook 1955, Eadie and Hamilton 1958, Wright and Coulter 1967, Kelly 1977, and Douglas and Strickland 1987). Counts of corpora lutea indicated fecundity rates (mean number of corpora lutea x proportion of females ovulating) of 3.0 for females ≥1 yr in Maine (1978-81, _n_ = 141, 95% ovulating; Shea et al. 1985) and 3.3 in Ontario (1972-84, _n_

= 1173, 97% ovulating; Douglas and Strickland 1987). A recent study in southcentral Maine (Arthur and Krohn 1990) documented annual rates of natal denning for adult females (≥2 yrs.) averaging 34% (range 0-75%). Although based on small annual samples (range of n = 1-5, total n = 16), these rates are substantially lower than reported proportions of females ovulating.

Kelly (1977) estimated mean annual survival rates for juvenile and adult fishers from 3 regions of New Hampshire. He determined the expected number of juveniles using ovulation rate and the number of radio-collared or harvested adult females, and he calculated survival rate as the ratio of juveniles observed in the harvest per expected. Survival rates for adults were estimated using catch-curve analysis (Robson and Chapman 1961), but Kelly (1977) did not address key assumptions.

My study used radiotelemetry data from 1984-89 to monitor the reproductive histories and survival of female fishers in Waldo County, Maine. The objectives were to (1) estimate fall recruitment and annual survival rates for the fisher population in southcentral Maine, (2) estimate the recruitment needed to maintain the population, (3) estimate the population trend, and (4) compare the estimated trend to independent indices of population trend.

METHODS

Estimating Recruitment

Between March 1984 and December 1989, 31 female fishers were captured and fitted with radio collars according to procedures described by Arthur (1988), except that in 1989 the transmitter collars included a leather insert that would decay and separate if the animals were not recovered (cf. Hellgren et al. 1988). A first premolar was removed, and one person prepared all teeth and interpreted cementum annuli using procedures of (Strickland et al. 1982). Radio-collared fishers were located using 2-element Yagi antennas from small aircraft or by triangulation on the ground (Arthur et al. 1989a) at least once per week and often every 3-5 days during the trapping season (late Oct-early Dec). Adult females were located daily, when possible, from late February to mid June to determine if they consistently rested in the same hollow trees, presumed to be natal dens (Arthur and Krohn 1990).

In 1988 and 1989, den cavities were searched when the female was absent to estimate litter size by verifying the presence of offspring 6-8 weeks after the initial den was first used (spring recruitment rate = denning rate x litter size). I did not attempt earlier visits for fear of delayed return by the mother during the cold, damp weather. Kits were sexed and fitted with ear tags (Monel #1, National Band and Tag Co., Newport, KY). Because tissue infection is suspected in loss of ear tags (Newby and Hawley 1954), ear tags were rinsed with isopropyl alcohol before being attached to the base of the anterior edge of the ear. Ancillary to estimating spring recruitment in wild fishers, I obtained data on litter sizes and neonatal mortality of captive fishers from one fur farm in each of Massachusetts, New York, and Wisconsin.

I defined fall recruitment rate as the mean number of kits per all adult females at the start of the trapping season (late Oct) (spring recruitment rate x summer survival of kits). Minimum survival rate of kits to late October was verified by livetrapping in and near home ranges of mothers in September and October and by recovering ear tags of kits captured during the trapping season. Prior to trapping season, a notice offering a $20 reward for the return of ear tags and radio collars from trapped fishers was distributed to trappers living in, or who had caught fishers in, WMU 7.

Estimating Survival

Survival rates for juvenile (7.5-12 months of age) and adult ($\geq$12 months) female fishers were calculated for 1984-89 (Trent and Rongstad 1974) using MICROMORT (Heisey and Fuller 1985), with the day following the end of trapping season being the anniversary date. Date of death was assigned as the midpoint of dates from consecutive triangulations (live, then dead) or from trapper returns. Each year was divided into trapping (36-42 days) and nontrapping (323-329 days) intervals in which the daily survival rate was assumed to be constant for each age class (Heisey and Fuller 1985). Thirteen (81%) of 16 female mortalities occurred during the trapping season. To determine if the mortality rate was constant during this interval, I divided the trapping season each year into thirds and within each calculated the proportion of available fishers trapped for each age class, pooling over 1984-89 because of small annual samples. The null hypothesis of a constant proportion of harvest among the three periods was tested using the normal approximation of a contingency table analysis (Zar 1984:400-401).

Calculating an adult survival rate assumed that yearling females (age of 1st breeding) had the same survival rate as older females (potentially parous). Pooling 1985-89 within age class because of small annual samples, I tested for differences in interval survival distributions between the 2 age classes using a log rank test (LIFETEST procedure; SAS, Inc. 1985) to see if pooling age classes within intervals was reasonable. LIFETEST can include right-censored animals (radio contact lost). However, I had to assume left-censored animals (radiocollared after start of interval) were alive at the start of the interval, giving a positive bias to survival in the test because some fishers may have died during the interval but prior to when livetrapping occurred. Juveniles were assumed to have been born on 15 March (see Chapter 2), and their survival until the start of trapping season was subsumed in the recruitment estimate (hence, their nontrapping interval was 95-101 days). Juveniles became adults on 15 March of the year following their birth.

Estimating Population Trend

Henny et al. (1970:691, equation 1) presented a discrete approximation to Lotka's equation for a stationary population (finite population increment [λ] = 1, stable age distribution) using age-specific rates of recruitment (m_x) and survival (s_x). Assuming a constant recruitment rate for individuals that produce young at the end of their second year and have a constant survival past age 1, Lotka's equation simplifies to:

$$1.0 = \overline{m}S_oS + S, \quad (1)$$

where S_o = juvenile female survival (<1 year), S = adult female survival ($\geq$1 yr), and $\overline{m}$ = mean fall recruitment rate (kits per all females $\geq$2 yrs).

Equation (1) can be solved for $\overline{m}$ (Henny et al. 1970) to examine the recruitment needed to maintain a stationary population given estimates of survival. Averaging the age-specific recruitment to calculate $\overline{m}$ required that whelping be distributed equally among females $\geq$2 years. The proportion of years that a female whelped was calculated to see if reproduction was effected by only a few of the females monitored. Kit survival until trapping season was assumed to be constant for all litters. Estimates of S_o and S and their respective 95% confidence limits were used in equation (1) to calculate the $\bar{m}$ needed for a stable population, and the estimated range of recruitment during 1988-89 was then compared to the predicted $\bar{m}$.

Given estimates of recruitment and survival, Lotka's equation for fishers is rearranged (cf. Henny et al. 1970) and solved for λ using a quadratic equation:

$$\lambda = [S+(S^2+4\bar{m}S_oS)^{1/2}]/2 \quad (2)$$

Annual range of fall recruitment (upper and lower limits) was calculated from maximum and minimum estimates, respectively, of mean litter size and summer survival of wild kits (1988-89) and annual estimates of denning rate for 1985-89. Annual midpoints and upper and lower limits of fall recruitment were then combined with estimates and upper and lower 95% confidence limits, respectively, of average S_o and annual S in equation (2) to estimate annual λ ($\pm$ range) for 1985-89.

Observed Population Indices

Catch per unit effort (CPUE) is an index to population density (Caughley 1977:17-18). Livetrapping methods in September and October were standardized during 1985-89, with many of the same trap sites used each year (1984 CPUE excluded because of nonstandard methods). Traps were generally spread throughout the study area, although some traps were located based on the distribution of radio-collared individuals. Traps usually remained at the same site during the entire trapping period. Sprung traps or nontarget catches were subtracted from the number of available trapnights, as were repeat catches of individual fishers, and CPUE each year was calculated as fishers caught per 100 trapnights. Trend in capture rate was tested by Spearman rank correlation (Conover 1980:252-256) using SYSTAT (Wilkinson 1989:682).

The MDIFW tabulates harvest data to derive indices to harvest success by trappers, which should correspond to trends in population. In addition to fishers, terrestrial furbearers in WMU 7 whose pelts are sealed by MDIFW include bobcats (Felis rufus), coyotes (Canis latrans), gray foxes (Urocyon cinereoargenteus) red foxes (Vulpes vulpes), and martens (Martes americana), and prior to the 1989 trapping season, raccoons (Procyon lotor). Trends in fisher harvest, number of trappers catching ≥1 fisher, and the ratio of trappers catching ≥1 fisher per trappers catching ≥1 terrestrial furbearer (fisher:terrestrial species) during 1977-89 (MDIFW, unpubl. data) were tested by Spearman rank correlation. Trends in CPUE and harvest indices were then compared to the estimated population trend.

RESULTS

Recruitment

Six adult females were monitored 1 year and 6 were monitored 2-5 years for a total of 25 fisher-seasons (season = Mar-Jun denning period) (Appendix G). Annual rates of natal denning for 1984-89 averaged 54.5% (range 0-100%) (Table 5). Arthur and Krohn (1990) excluded 2 lactating females (F401 in 1985 and F461 in 1986) from their analysis of denning rate because the fishers did not return to natal dens after being livetrapped. I included these 2 female in the current analysis as having successfully reproduced because they were lactating, suggesting that they whelped and suckled young.

Denning rate seemed to be affected by both year (Table 5) and age of female (Fig. 6), but sample sizes are too small to test for interactions of age and year. Two and 3-year-old females composed 72% of the annual harvest of females $\geq$2 yrs in WMU 7 (MDIFW, unpubl. data, 1982-84; total n = 72), so a significantly lower denning rate by these females would strongly affect the average denning rate of the population. Annual samples for denning rate were small; if the binomial distribution is used to construct 90% confidence intervals around annual rates (Conover 1980:100), only 1984 and 1985 exclude rates of >0.93, which is approximately that of ovulation (Shea et al. 1985).

Table 5. Annual and cumulative rates of natal denning (percentage of female fishers ≥2 yrs observed at dens during March-June) in Waldo County, Maine, 1984-89.

	1984	1985	1986	1987	1988	1989
annual denning rate (*n*):	0 (1)	33 (6)	67 (6)	60 (5)	100 (4)	67 (3)
cumulative denning rate (*n*):	0 (1)	29 (7)	46 (13)	50 (18)	59 (22)	60 (25)

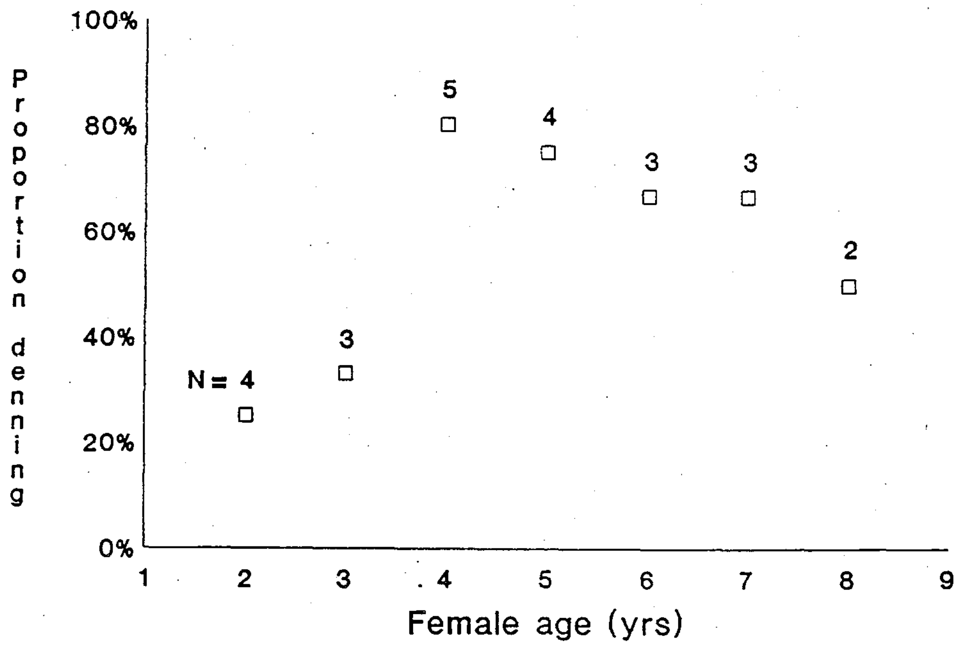


Fig. 6. Age-specific denning rate of 11 radio-collared adult ($\geq$2 yrs) female fishers (6 monitored >1 yr) in Waldo County, Maine, 1984-89.

However, 5 of 6 years were consistent in having rates substantially lower that ovulation, so I used the cumulative denning rate (weighted mean) of 0.60 (Table 5) as the average annual denning rate.

Litters of 4 females in 1988 were examined in early-mid May (composition = 1M; 1M; 1M,1F; and 2M,1F). One litter was handled on or following the day that the female moved the kits to a new den. A single male kit was found in the new den, but livetrapping within the female's home range in September produced a juvenile female that remained in her home range until late January 1989 (see Chapter 2). Because I may have missed other kit(s) in her litter, I assigned her a litter of 1-2 kits; thus, mean litter size in 1988 was 1.8-2.0 kits per female that whelped. A single litter (2M,1F) was handled in late April 1989. Mean litter size for 1988-89 combined was 2.0-2.2 kits per female that whelped (Table 6). Litter size from captive fishers in Massachusetts and New York ($\bar{x}$ = 2.9, range 1-4, n = 19) was not different than litter size in wild fishers (U = 3.62, 3 df, P = 0.30), and age of female did not affect litter size (Appendix H).

Based on recovery of ear-tagged kits (Appendix I) and the extra female kit captured in September, minimum survival rate from spring recruitment until start of the fur trapping season in 1988 was 4/7 = 0.57 or 5/8 = 0.63. In 1989, 2 of 3 ear-tagged kits were livetrapped prior to the fur trapping

Table 6. Litter size per denning female and summer survival of fisher kits used to calculate recruitment rates (kits per all females ≥ 2 yrs). Denning rate was assumed to be 0.60 of the females per year[a] for all calculations.

Year(s)	No. of litters	Litter size[b]	Summer survival[c]	Fall recruit.[d]
1988	4	1.8-2.0	0.57-1.0	0.6-1.2
1989	1	3.0	0.67-1.0	1.2-1.8
Total	5	2.0-2.2	0.60-1.0	0.7-1.3

[a]From Table 5.

[b]Kits ear-tagged at natal den when 6-8 weeks old (late Apr-mid May). Range of spring recruitment rate is calculated as denning rate x upper and lower range in litter size.

[c]Summer is the period between examining kits at natal den until the start of trapping season in late October. Low value of range is the minimum estimate from recovery of ear-tagged kits, and upper value is assuming all kits survived.

[d]Lower value of range is denning rate x lower range of litter size x minimum estimate of summer survival. Upper value of range uses upper range of litter size and assumes all kits survive until fall.

season for a minimum survival rate of 0.67. The minimum survival rate for summers 1988-89 was 6/10 = 0.60 or 7/11 = 0.64. A conservative rate of fall recruitment for 1988-89 ranged from 0.7-1.3 kits per adult female (Table 6).

Survival

The proportions of radio-collared females trapped during each third of the trapping season were not different for juveniles ($\underline{X}^2$ = 2.81, 2 d.f., $\underline{P}$ = 0.25) or adults ($\underline{X}^2$ = 2.74, 2 d.f., $\underline{P}$ =0.25), so a single trapping interval was used. Survival distributions of yearling vs. older females were not different during nontrapping (log rank test, $\underline{X}^2$ = 0.21, $\underline{P}$ = 0.65) or trapping ($\underline{X}^2$ = 2.1, $\underline{P}$ = 0.15) intervals, so those age classes were pooled within intervals to estimate S. Because of small annual samples of juvenile females (none in 1986), deaths and radio-days were pooled over years 1984-89, within trapping and nontrapping intervals, to calculate an average rate of survival (S_o; Table 7). Confidence limits on S_o were wide, and survival distributions for the juvenile sexes were not different within nontrapping (log rank test, $\underline{X}^2$ = 0.30, $\underline{P}$ = 0.59) and trapping ($\underline{X}^2$ = 0.30, $\underline{P}$ = 0.58) intervals, so I pooled data within trapping and nontrapping intervals for male and female juveniles and recalculated S_o for all juveniles (Table 7). Annual samples of adult females also were small, so I pooled over 1984-89 to estimate adult survival (S; Table 7).

Table 7. Annual and average annual survival rates of adult females ($\geq$1 yr; S) and average survival rates for juvenile (<1 yr; S_o) fishers in Waldo Co., Maine, 1984-89. Pooled rates include deaths and radio-days over all years within trapping and nontrapping intervals. See Appendix J for interval rates.

Survival Class	n[a]	deaths	Radio-days alive	Survival rate [95% CL][b]
Juv. Fem. 1984-89	18	8	587	0.27 [0.11,0.72]
All Juv. 1984-89	42	24	2,105	0.33 [0.21,0.52]
Ad. Females 1984	1	0	212	1.0
Ad. Females 1985	9	3	1,519	0.58 [0.30,1.0]
Ad. Females 1986	9	0	2,364	1.0
Ad. Females 1987	7	1	2,355	0.84 [0.59,1.0]
Ad. Females 1988	7	3	1,577	0.63 [0.34,1.0]
Ad. Females 1989	9	2	1,405	0.42 [0.11,1.0]
Ad. Fem. 1984-89	42	8	9,432	0.74 [0.59,0.91]

[a]Individuals monitored (7 adult females were monitored >1 yr).

[b]Calculated using MICROMORT (Heisey and Fuller 1985).

Radio contact was lost for 12 adult females, either because they slipped their radio collars ($\underline{n}$ = 9) or transmitters apparently failed ($\underline{n}$ = 3). In addition, 3 juvenile females slipped their collars. Of the 15 censored fishers, 3 (2 adults, 1 juvenile) were recaptured by project personnel and 2 adults were captured by fur trappers; these 5 individuals were included in survival calculations as having been alive during interim periods of not being monitored. The remaining censored fishers ($\underline{n}$ = 10) were assumed to have survived to their last day of valid radio contact and then dropped from the model; this would give a positive bias to survival if any fishers had died as a result of censoring, and a negative bias if censored fishers lived but were not vulnerable to recovery. One juvenile male was lost from radio contact twice (slipped collar, failed transmitter) but was recovered both times by livetrapping.

Estimated Population Trend

All females monitored for 2-5 years whelped at least once ($\underline{n}$ = 6 individuals over 19 fisher-seasons), as did 3 of 6 monitored for only 1 year. I assumed that all females $\geq$2 years whelped with equal frequency and averaged m_x to $\bar{m}$.

Comparing my estimate of fall recruitment (both sexes in litter size) directly to 2X $\bar{m}$ (female segment only) assumes an even sex ratio at recruitment. Douglas and Strickland (1987:516) reported that the sex ratio of fisher kits at birth in captivity was not significantly different from 50:50. Data I obtained from fur farmers in Massachusetts (n = 5 litters), New York (n = 1), and Wisconsin (n = 1) were similar (13M:11F). My sample of 5 litters from natal dens in the wild was 7M:4F. I assumed an equal sex ratio at birth and that sex-specific survival was equal until fall recruitment.

Assuming a stable age distribution, 2.1 kits per all females $\geq$2 yrs must survive until fall to maintain the fisher population, given the pooled estimates of S_0 (all juveniles) and S (Fig. 7). The lower confidence limits of survival would require a fall recruitment rate of 6.6 kits per all females, whereas the upper confidence limits (Fig. 7) would require only 0.38 kits per all female. Observed recruitment ($2\bar{m}$ = 0.7-1.3; Table 6) and pooled estimates of S_0 and S predicted λ = 0.84-0.91. With maximum observed litter size (2.2 kits per female; Table 6), a 100% denning rate (similar to ovulation rate), and 100% kit survival until fall recruitment, pooled estimates of S_0 (all juveniles) and S predict λ = 1.01. Estimates of λ calculated from annual estimates of recruitment and survival during 1985-89 indicated a declining population during 3 of 5 years (Fig. 8); 1984 was excluded because denning rate was 0% (Table 5).

Observed Population Trend

CPUE for fall livetrapping showed a downward trend

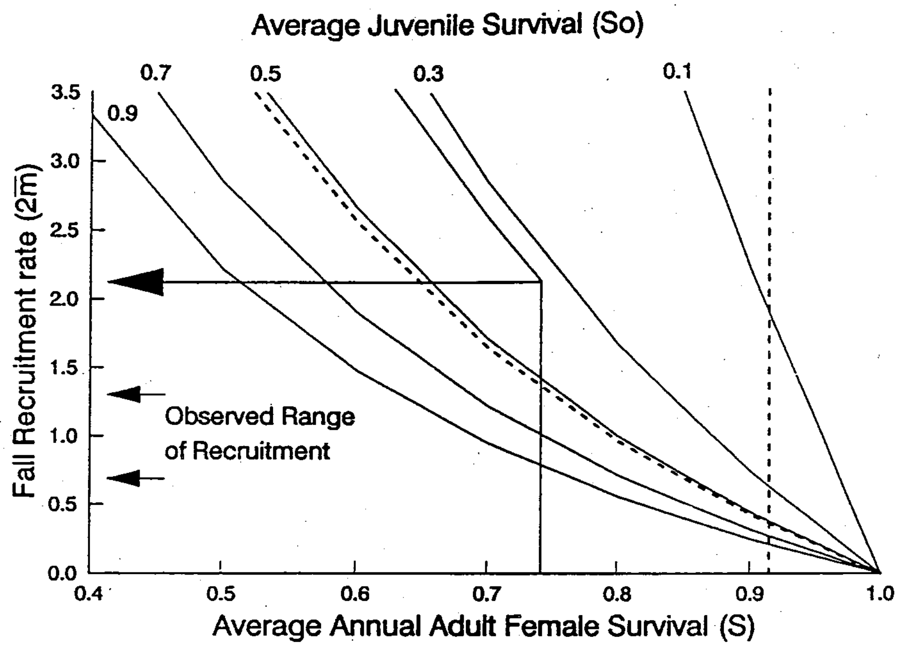


Fig. 7. Isopleths are combinations of fall recruitment and average survival of fishers that produce a stable population ($\lambda = 1$). Estimates of S_0 (0.33, both sexes) and S (0.74) from 1984-89 require a fall recruitment rate of 2.1 kits per all females to maintain the population. The region within the dashed boundary is the zone of stability allowed by the upper 95% CLs of S_0 (0.52, both sexes) and S (0.91).

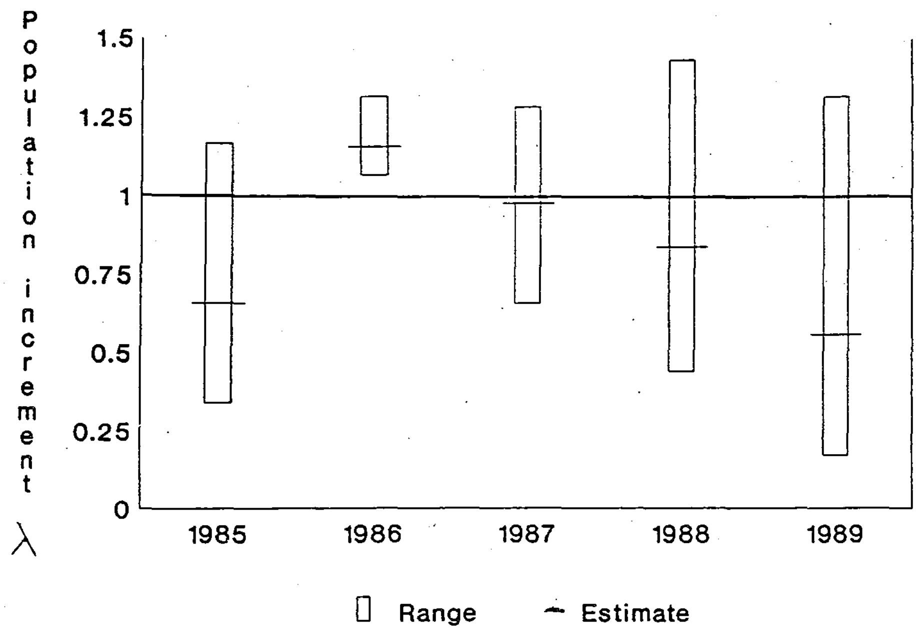


Fig. 8. Annual estimates of population increment (λ) for fishers in Waldo County, Maine, 1985-89.

during 1985-89 (Fig. 9A). Trend in fisher harvest and number of trappers catching ≥1 fisher in WMU 7 also declined during 1977-89 (Fig. 9B). The ratio of successful trappers (fisher:terrestrial species) declined from 1977-86 (r_s = -0.890, n = 10, P = 0.0007) but increased sharply in 1987 (Fig. 9B); this increase in harvest ratio may have resulted from the decline in price paid for pelts of terrestrial species since 1986 (MDIFW, upubl. data) and a relative increase in effort toward the more valuable fishers.

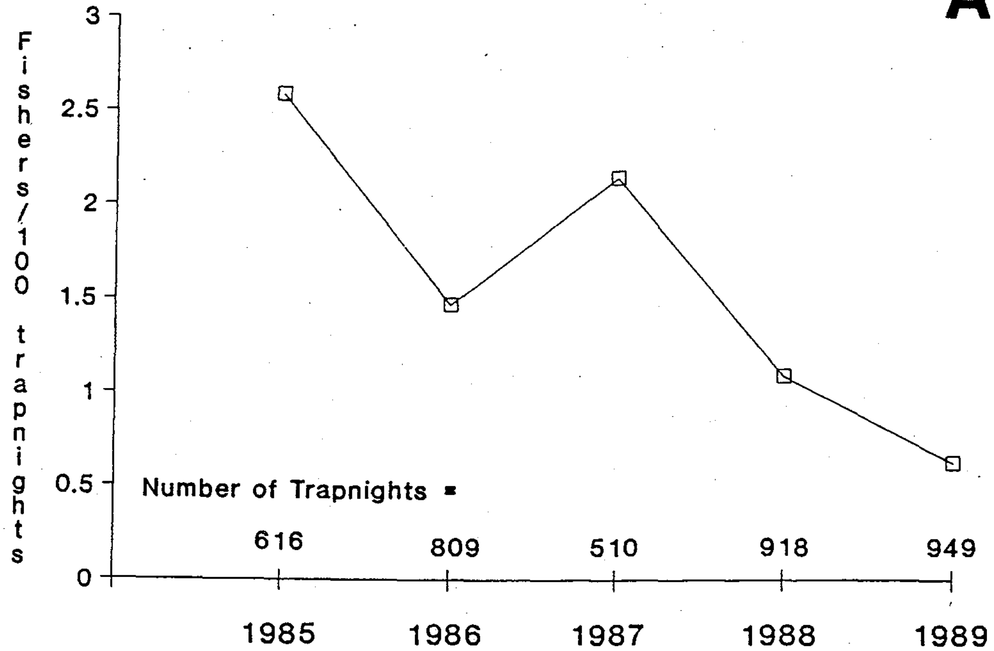
DISCUSSION

Radiocollaring effects

Estimates of annual denning rate would be biased if capturing, radiocollaring, or observing females adversely affected reproduction, particularly because several individuals were monitored over multiple years (Appendix G). Individuals were captured from 1-10 times by livetrapping or darting from trees; 24 of 28 livetrapping recaptures included anesthesia and processing. No female showed signs of physical stress from being radiocollared. Natal denning occurred from early March to early June (Chapter 2). Three of 5 females processed between 6 March and 17 April reproduced (denned later that spring or were lactating and did not abandon natal dens) and 2 did not; this excludes 2 females initially captured in April that may have abandoned

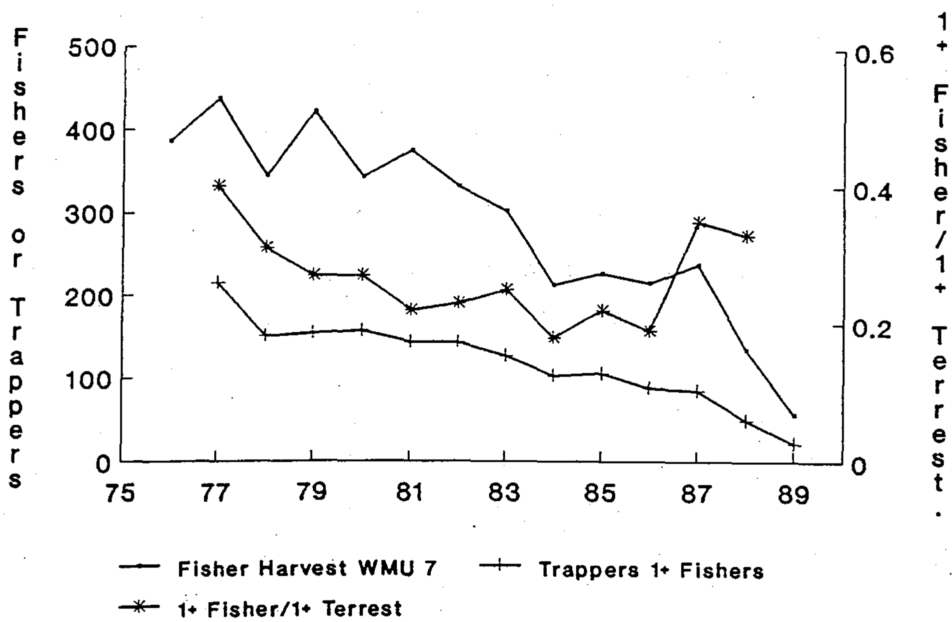
Fig. 9. Observed trends in the fisher population in Waldo County, Maine, based on: A - catch per unit effort livetrapping (fishers/100 trapnights) during Sept-Oct, 1985-89 (r_s = -0.900, P = 0.05, 1-tailed), and B - trends in fisher harvest (r_s = -0.865, P < 0.0005, 1-tailed) and number of trappers catching ≥1 fisher (r_s = -0.963, P < 0.0005, 1-tailed) in Wildlife Management Unit 7, southcentral Maine, 1976-89. The ratio of trappers catching ≥1 fisher per trappers catching ≥1 terrestrial species (bobcats, coyotes, gray and red foxes, martens, and raccoons) declined during 1977-86 (r_s = -0.890, P = 0.0007). (Unpubl. data, Maine Dept. Inland Fish. and Wildl.; 1989 data are preliminary).

A



Fishers/100 trapnights
3
2.5
2
1.5
1
0.5
0
Number of Trapnights =
616
809
510
918
949
1985
1986
1987
1988
1989

B



Fishers or Trappers
500
400
300
200
100
0
1+ Fisher/1+ Terrest.
0.6
0.4
0.2
0
75
77
79
81
83
85
87
89
Fisher Harvest WMU 7
Trappers 1+ Fishers
1+ Fisher/1+ Terrest

young as a result of capture but whose histories were unknown (Arthur and Krohn 1990). Similarly, 9 of 15 females processed between 25 September and 25 February denned the following spring. The denning rate for females monitored a single year (0.66; n = 6) was not different from the rate (0.58; n = 19 fisher-seasons) for females monitored multiple years (Z corrected for continuity = -0.096, 2-tailed, P = 0.46; Zar 1984:396). Thus, date of capture and duration of being radiocollared had no apparent effect on whelping for those females with known histories.

Radiocollaring probably did not influence natal denning by adult females. Arthur and Krohn (1990) found that 55% of adult females caught by trappers in central Maine in 1987 had enlarged mammillae (n = 11; see Chapter 4) compared to the 60% denning rate for that year (n = 5). In 1988, I found placental scars in 89% of females $\geq$2 yrs. from central Maine (n = 9) compared to a denning rate of 100% (n = 4), and in 1989 placental scars occurred in 67% (n = 12) of the females compared to a denning rate of 67% (n = 3) (see Chapter 4).

Recruitment

Estimates of litter size at the den should be made when kits are still relatively docile (ca. 6 weeks old) and preferably when the mother is not moving kits to a new den. Observing mothers and kits by stalking in summer was not effective for estimating kit survival because kits were frequently inside cavities, or the mothers detected people approaching and avoided observation (Appendix K). Recapture of ear-tagged kits in the fall is a direct means to estimate minimum survival until trapping season, but not all kits will be caught, and some may lose their ear tags. Tetracycline might be useful for positive identification of some kits (Appendix L). Radiomarking kits would allow estimation of cause-specific survival; however, an external transmitter on kits might present a danger of entanglement, and the side-effects of surgically implanting a transmitter in kits requires testing prior to field use.

Denning rate could be used to estimate whelping rate if neonatal mortality does not occur before denning can be determined for radio-collared females. The extent of neonatal mortality in wild fishers is unknown, but it is common in captive fishers (Hodgson 1937, Hall 1942). Leonard (1986) reported the loss of a litter ca. 36 hours after birth by a female that whelped in captivity soon after being captured. Fur farmers in Massachusetts, New York, and Wisconsin lost 6 of 24 litters within a few days postpartum, 22 of which were from females caught in the wild the previous autumn. Thus, until litter loss of wild fishers prior to 3 days of age (see Chapter 2) is quantified, denning rate can only be a minimum estimate of whelping rate.

Estimating summer survival of kits using Kelly's (1977) methods would be useful to managers for estimating trends in kit survival, but the ratio of kits per adult female assumes a constant reproductive rate, no mortality of adult females between birth of kits and trapping season, and equal vulnerability of adult females and kits to trapping. My data suggest that denning rate may vary substantially from year to year, and Krohn et al. (1989) suggested that adult female fishers are less vulnerable to fur trapping than juveniles. Eartagging and recapture of kits provides a conservative estimate of fall recruitment rate.

Survival

Although sample sizes were small, I calculated annual estimates of S to detect yearly changes that might occur because the population model is most sensitive to changes in S. To pool data on adult females and juveniles among years for trapping intervals, I assumed the harvest effort was constant each year. Trapper effort has not been directly estimated in Maine, but indices to effort have been monitored, and the number of successful fisher trappers in WMU 7 has declined steadily since 1982 (Fig. 9B). Clark (1985) found that 71% of 932 Maine trappers surveyed obtain information on pelt prices from local furbuyers prior to trapping season, and some trapping effort is influenced by price. A survey of average prices paid for pelts of female fishers by furbuyers in Maine showed an increase from $152 to $183 during 1983-86 (1984 missing) and a decline to $91 by 1988 (MDIFW, unpubl. data). Because the reward offered for the return of marked animals was small ($20) relative to average pelt price, I doubt it influenced harvest effort or rate. Harvest effort seems to have dropped during 1985-89, but the magnitude of change cannot be estimated from available indices to effort.

My estimates of survival were independent of harvest ratios. Kelly (1977) estimated survival of adult fishers using catch-curve analysis. However, he did not address the assumptions of equal juvenile cohorts in past years, equal vulnerability among classes, and constant adult survival for estimating survival from the standing age distribution in the harvest (Robson and Chapman 1961). Annual estimates of survival for adult females may have changed over the years I examined (Table 7), and relative vulnerability of age-sex classes may also have varied. Use of harvest ratios to estimate survival rates is unwarranted without further data to verify assumptions of equal harvest effort and vulnerability.

Harvest management

The model for a stable population (Fig. 7) and annual estimates of λ (Fig. 8) suggest that the population is declining, even after pooling juvenile sexes (which increases S_0) and considering that S_0 and S might be positively biased because of censored animals. Juvenile fishers commonly disperse 10-15 km from their mother's range

(S. M. Arthur, MDIFW, pers. commun.; Paragi, unpubl. data), and the harvest density for fishers is estimated to be equally high surrounding the study area (Clark 1986); therefore, it seems unlikely that immigration from adjacent areas could compensate for the low survival of fishers.

Because estimated and observed trends in population declined, I conclude that the fisher population in Waldo County declined over 1985-89. Although my estimates of $\overline{m}$, S_o, and S are highly variable, even when survival estimates are pooled over years, Figs. 7 and 8 suggest a declining population. The decline in CPUE is not strong, but it is consistent with the predicted decline in population; I assumed CPUE was linearly related to population density, at least within the range of my data. Whether age- or sex-specific differences in vulnerability to livetrapping occur in fishers is unknown. Krohn et al. (1989) suggested that adult females are less vulnerable to fur harvesting than adult males or juveniles, and Arthur et al. (1989b:fig. 3) found that adult females use overlapping home ranges in consecutive years. Livetrapping in home ranges of adult females may bias CPUE negatively.

The strong decline in trapper success (number catching $\geq$1 fisher per number catching $\geq$1 terrestrial species) from 1977-86 suggests a decreasing availability of fishers to be captured, and I suspect this continued through 1989. The harvest ratio may be less sensitive to changes in fur prices (hence effort) and more indicative of trend in fisher population than either fisher harvest or number of successful fisher trappers. Many trappers that pursue terrestrial furbearers in WMU 7 will also set fisher traps and will use the same trap locations year after year, particularly those successful for fishers.

A stable age distribution might be an unreasonable assumption for a harvested population if harvest effort and vulnerability are changing. Douglas and Strickland (1987) suggested that trapping intensity can influence harvest composition and age structure of the population. However, furbearer managers must make decisions with the information at hand. Harvest effort in Maine was not estimated directly, and annual samples for estimating survival were too small to test for annual changes in vulnerability among age-sex classes (Krohn et al. 1989).

MANAGEMENT IMPLICATIONS

Fall recruitment rates for fishers in Waldo County (0.7-1.3 kits per all females ≥2 yrs) were substantially lower than fecundity rates for southcentral Maine (3.0 corpora lutea per female ≥1 yr, Shea et al. 1985; see Chapter 4). Ovulation rates are commonly measured in fishers and have been used in modeling harvest dynamics in regions with harvest densities lower than southern Maine (e.g., Douglas and Strickland 1987). The recruitment rate in southcentral Maine seems inadequate to produce a stable population with the current intensity of harvest. Harvest accounted for 40 (80%) of 50 mortalities of radio-collared fishers in the study area, 1984-89 (Maine Coop. Fish Wildl. Res. Unit, unpubl. data). The degree to which trapping and natural mortality compensate each other is unknown (Powell 1979, Douglas and Strickland 1987), but managers can control harvest much more easily than recruitment. The increasing human density in southern Maine means that more dirt roads will be maintained or paved to allow faster travel to nearby population centers, likely increasing the fisher mortality caused by vehicles. Because fishers are K-selected mustelids (King and Moors 1979) and were once extirpated from much of Maine (Coulter 1960), prudent management would be to assume the population is declining and reduce harvest effort toward fishers in southcentral Maine.

Managing to prevent overharvest requires monitoring of population characteristics. The current lack of techniques with which to precisely determine population size or growth rate for fishers may preclude calibrating a population index, but historical data on a harvest ratio such as juveniles per adult female may be useful for achieving harvest objectives (e.g., Douglas and Strickland 1987:523-525), even if cause and effect cannot be explicitly defined. Means of estimating trapper effort in Maine are being developed (K. D. Elowe, MDIFW, pers. commun.) and may allow better interpretation of harvest ratios.

A better knowledge of the ecological factors that affect denning rate (implantation, parturition, and neonatal survival) in fishers would contribute to the understanding of population dynamics. Body condition likely determines whether implantation occurs. Almost all female fishers will mate in spring and maintain blastocysts for 10-11 months because mating is not costly (Gittleman and Thompson 1984) and the females cannot predict the food supply (hence their body condition) the next winter when they implant. If food resources are scarce, delayed implantation has provided an energetically efficient means of terminating pregnancy before the demands of late gestation and lactation (Sadlier 1969, Bunnel and Tait 1981, Gittleman and Thompson 1984); however, a female must breed every year to realize this advantage. In black bears (Ursus americanus), reproductive success corresponded to autumn weights of females, which depended on availability of mast crops (Rogers 1976, Elowe and Dodge 1989). Another delayed implanter, the stoat (Mustela erminea), had consistently high ovulation rates, but density of juvenile stoats corresponded to density of the principal prey of female stoats during gestation and lactation (King 1981).

Managers might use winter energetics of fishers to predict reproductive success from body condition. Fasting endurance of fishers, based on fat reserves at any one time, probably is short relative to duration of winter conditions (Dec-Mar in Maine) because fishers remain active except in severe weather (Kelly 1977, Powell 1982; cf. Buskirk and Harlow 1989). Increasing snow depth hinders movements by fishers, causing them to change gaits and increase energy expenditure (Raine 1983). A regional index to winter severity that incorporated the sinking depth of female fishers in snow and their lower critical temperature (Powell 1982:167) might be used in conjunction with other indices as a tool for predicting sustainable harvests of fishers and adjusting harvest regulations for optimum yield.

IV. AN EVALUATION OF PLACENTAL SCARS AND MAMMILLAE AS INDICES TO FISHER REPRODUCTION

An ideal index to reproductive rate of a population (i.e., fecundity rate) provides the proportion of females reproducing (i.e., fertility rate) and their mean litter size at birth. Furbearer managers often obtain reproductive data from carcasses of animals collected from hunters and trappers (e.g., Payne 1982, Gilbert 1987). The reproductive tracts of fall-caught fishers contain information on two reproductive sequences because fishers are delayed implanters that breed in the spring and give birth almost a year later (Hall 1942, Hamilton and Cook 1955, Wright and Coulter 1967). Counts of corpora lutea (CL) measure ovulation rate, and counts of blastocysts (BC) measure fertilization; both indicate the potential rate of implantation for the next spring (Gilbert 1987). Placental scars (PS), from the past spring's reproduction, often occur as darkened areas at sites of implantation on the uterine horns (Kirkpatrick 1980:102). If prenatal losses occur (e.g., Brambell 1948), PS should more closely indicate the proportion of females whelping and their mean litter size at birth than CL or BC because PS are formed during or close to parturition. Although PS have been observed in mustelids during autumn and early winter (Wright and Rausch 1955, Wright 1966, Rausch and Pearson 1972), it has been suggested that some scars may fade before autumn (Madsen and Rasmussen 1985:146, Gilbert 1987:187) or disappear if uterine tissue autolyzes (Wright and Coulter 1967:75).

Fishers have 4 inguinal mammillae (= teats) (Coulter 1966). Size of teats on live furbearers or their pelts has been used for classifying individuals as immature (nulliparous) or mature (parous) for several furbearers (Wright 1948, Petrides 1950, Newby and Hawley 1954, Magoun 1985), sometimes in combination with color of teats (Sanderson and Nalbandov 1973, Garshelis et al. 1988). Douglas and Strickland (1987:521) noted that teats of adult female fishers that had suckled young were sometimes distinguishable from those of nulliparous females, although not sufficiently to sort pelts by reproductive status. If teats of females that suckled young are distinct from those not suckling, then teats could be used to estimate the proportion of females reproducing.

A study in southcentral Maine during 1984-89 monitored female fishers with known reproductive histories and estimated litter size and rate of natal denning for a population of wild fishers using radiotelemetry (Chapter 3). My objectives here are to (1) report data on teat size of radio-collared females and on PS from harvested females concurrent with the telemetry study, and (2) evaluate PS counts and teat size as reproductive indices by comparing them to data from radio-collared fishers.

METHODS

Reproductive terms used in this study are defined in Table 8. Carcasses of female fishers were voluntarily submitted by trappers and furbuyers in central Maine during 1987-89 trapping seasons (late Oct early Dec). Most of the collection effort was directed toward the study area. Carcasses usually were retrieved and necropsied within 48 hours of capture. Skulls were boiled in water to remove premolars. One person prepared teeth and counted cementum annuli (Strickland et al. 1982) for all fishers.

I examined the external surfaces of uterine horns for darkened areas assumed to be PS (Coulter 1966, Kirkpatrick 1980), although they were not confirmed histologically. Each horn of the uterus was flushed twice with 10 ml of water from a hypodermic needle inserted into the junction of the Fallopian tube and the uterus (cf. Hamilton and Cook 1955:30-31). BC were collected in a Petri dish and identified using a 7-30X dissecting microscope (Gilbert 1987:fig. 8). Ovaries were removed from the bursae, hardened for ≥2 weeks in 10% formalin, and hand-sectioned with a scalpel into 1-mm slices along the longitudinal axis (Wright and Coulter 1967, Shea et al. 1985, Gilbert 1987). Sections were examined for corpora lutea under a dissecting microscope (Gilbert 1987:fig. 6). Transverse sections were

Table 8. Definition of key reproductive terms used in this study (corpora lutea = CL, blasocysts = BC, and placental scars = PS).

Term	Definition
Fertile female	A female with ≥1 of the reproductive indicator being discussed; i.e., each female is assessed with respect to each of CL, BC, and PS[a].
Mean litter size	Number of CL, BC, or PS per fertile female, respectively.
Fertility rate	Proportion of females that are fertile.
Fecundity	Mean number of CL, BC, or PS per capita (mean litter size x fertility rate).
Productivity	Kits per all females ≥2 yrs; at birth.
Parous	Suckled young the previous spring[b].
Nonparous	Did not suckle young the previous spring[b].
Nulliparous	Never suckled young.

[a]Because fishers first mate at age 1 and whelp at age 2 (Hall 1942, Eadie and Hamilton 1955, Wright and Coulter 1967), I assumed only females ≥1.5 yrs of age had CL or BC, whereas females ≥2.5 yrs could have PS.

[b]Females ≥2 yrs with known reproductive histories via radiotelemetry.

cut through luteal structures for closer examination in instances when >1 corpus luteum seemed to abut within a section. Uterine horns were split longitudinally (Payne 1982:42) and examined under a dissecting microscope for PS, which I defined as areas of granular, dark-pigmented material. All females were examined for PS, although I expected to find PS only in adult females ≥2.5 years of age. After examining tracts and finding darkened areas, I immersed the tracts in a fixative (AFA, Bouin's solution, or formalin), bleach (sodium hypochlorite), clearing agent (oil of wintergreen) (Kirkpatrick 1980), or a whole-tissue carmine stain (B. G. Wood, Univ. Maine, pers. commun.) to determine if darkened areas could be accentuated.

The difference between distributions of litter size based on BC and PS were tested with the Mann-Whitney U (Conover 1980:216-218) using SYSTAT (Wilkinson 1989:600) because counts were not normally distributed and had unequal variances (Zar 1984:130). A z-test corrected for continuity (Zar 1984:396) was used to test for difference in fertility rate.

Ancillary to this study, data on CL, BC, and PS were obtained from fishers harvested in New Hampshire (1987) and Vermont (1988) using the methods of this study (Crowley et al. 1990). Age-specific fertility rate and litter size based on the 3 reproductive indices were then compiled among Maine (this study), New Hampshire, and Vermont (S. K.

Crowley, Univ. Maine, pers. commun.).

Teats of radio-collared females were examined while fishers were anesthetized after being livetrapped or darted (Arthur 1988), 1984-89. Teats were measured by 1 of the 4 individuals that examined the fishers. Fishers caught by trappers were examined 24-72 hours postmortem; some had been frozen, and one was freshly skinned. Height (base-to-tip) and base length (anterior-posterior) of teats on female fishers were measured to 0.1 mm using a dial caliper. Data on teat size collected during 1984-87 were qualitative (S. M. Arthur, MDIFW, pers. commun.), whereas data from 1988-89 were quantitative. Teats were considered "enlarged" if >3 mm in either measurement.

RESULTS

One female with CL and BC was estimated to be age 0 from tooth cementum, and 3 females with PS were estimated to be age 1; ages of these females were revised by adding 1 year.

Placental Scars

PS were evident on the exterior of the uterine horns in 15 (75%) of 20 females ≥2 yrs examined during 1988-89 (Table 9). In 36 (95%) of 38 instances (n = 15 females with PS), PS on the exterior of the uterus corresponded to internal sites of granular, dark-pigmented material typically 2-3 mm

Table 9. Frequency of counts (number of reproductive indicators) and summary statistics for corpora lutea (CL), blastocysts (BC), and placental scars (PS) from female fishers[a] in central Maine, 1988-89.

	CL[b]		BC[b]		PS[c]	
count	1988	1989	1988	1989	1988	1989
0	1	0	3	3	1	4
1	1	1	2	2	0	3
2	1	5	0	4	3	1
3	9	12	5	9	2	3
4	6	6	8[d]	5	2	1
Litter size:						
Mode	3	3	4[d]	3	3	1,3
Mean	3.2	3.0	3.3[d]	2.9	2.9	2.3
Rates:						
Fertility	94%	100%	83%	87%	88%	67%
Fecundity	3.0	3.0	2.7	2.5	2.5	1.5
<u>n</u>	18	24	18	23	8	12

[a]Based on carcasses submitted by fur trappers.

[b]Age $\geq$1 yr.

[c]Age $\geq$2 yrs.

[d]Number of BC (4) > number of CL (3) in 3 uteri.

long and 1/4 the inner circumference of the horn (Fig. 10). If 2 or 3 sites occurred on a single horn of the uterus, they were always equally spaced (cf. Gilbert 1987:184). The darkened areas were evident even in tracts that were a dark maroon because of postmortem mixing of body fluids.

Modal number of CL and BC (3-4) were greater than those of PS (0-2) per all females (Table 9). This suggests that fertilized females that fail to implant (or that lose their litters prior to when PS form) cause most of the discrepancy between BC and PS. However, counts of BC in 1988 were not significantly greater than PS in 1989 in either fertility rate ($\underline{Z}$ = 1.15, $\underline{P}$ = 0.13) or litter size ($\underline{U}$ = 5.29, 3 df, $\underline{P}$ = 0.15). Fecundity and modal litter size based on PS were greater for females age 2 than females ages 3-9 for fishers from Maine, New Hampshire, and Vermont (Table 10). However, differences based on PS in fishers age 2 vs. age 3-9 were not significant for fertility ($\underline{P} \geq 0.11$) or litter size ($\underline{P} \geq 0.18$) in any state.

Placing uteri in preservative, clearing agent, or whole-tissue stain resulted in disappearance of PS in $\leq$10 min. Subsequent washing in tap water did not cause the darkened areas to reappear. PS were accentuated by immersion for ca. 5 min in Bouin's solution as the uterine horns became yellow, but PS disappeared after being immersed ca. 10 min.

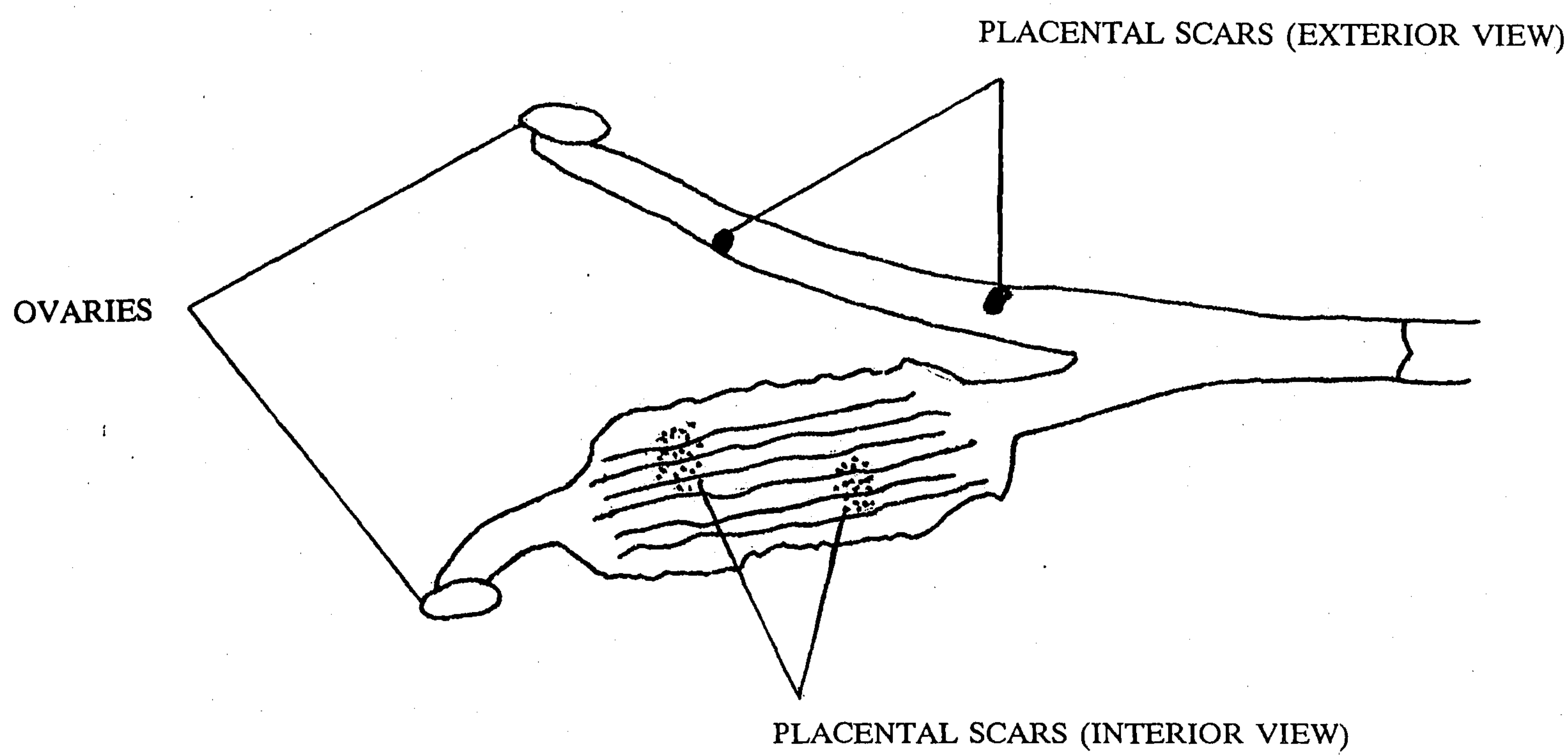


Fig. 10. Position of placental scars in the reproductive tract of adult (≥2 yrs) female fishers. Scale of figure is ca. 2X that of a tract from a parous female.

Table 10. Age-specific counts of placental scars in female fishers from Maine (1988-89), New Hampshire (1987)[a], and Vermont (1988)[a].

	Age 2 yrs			Age 3-9 yrs		
	ME	NH	VT	ME	NH	VT
Litter size:						
Mode	3	4	3	2	3	1
Mean	2.6	2.9	2.7	2.0	3.0	2.2
Rates:						
Fertility	83	56	24	57	40	20
Fecundity	2.2	1.6	0.7	1.1	1.2	0.4
_n_[b]	12	16	25	7	15	25

[a]Data courtesy of S.K. Crowley, Univ. Maine (pers. commun.).
[b]Number of females examined. One female from Maine was excluded from this analysis because age was not estimated using cementum annuli.

Teat Size

Qualitative judgement and measurements on teat size of 3 radio-collared adults with known reproductive histories (n = 11 fisher-years, 1985-89) suggested that the enlarged teats of females that had suckled young regressed in size prior to the following whelping period (March) (e.g., Fig. 11) and became larger with subsequent reproduction. One parous female that did not whelp the following spring did not have large teats during summer and fall.

Height of teats was usually greater than length at base, and size of anterior teats was ≥ posterior teats. Using height alone, juvenile (<1 yr) and yearling females typically had small teats that were difficult to find except by careful palpation; none had enlarged teats (n = 26 examined mid Sep-late Nov, 1988-89). Seven parous females that suckled kits had teats larger than a female without kits; 3 of the parous females measured during the trapping season had teats 6-9 mm tall (Fig. 12). Teat height of nonparous and parous females did not overlap, and teats ≥6 mm corresponded to females that had suckled young during the previous spring.

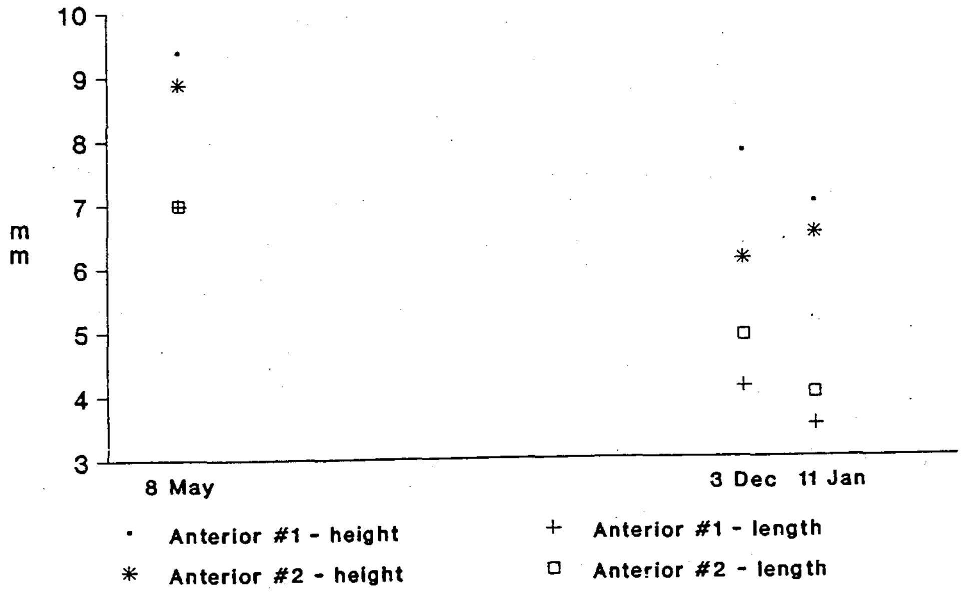


Fig. 11. Height and length of the anterior teats on a 6-yr-old radio-collared female (F325) in Waldo County, Maine that suckled 3 kits in 1988. Measurements in January 1989 were postmortem. Posterior teats were smaller in all measurements but also regressed in size. The 2 length measurements overlapped on 18 May.

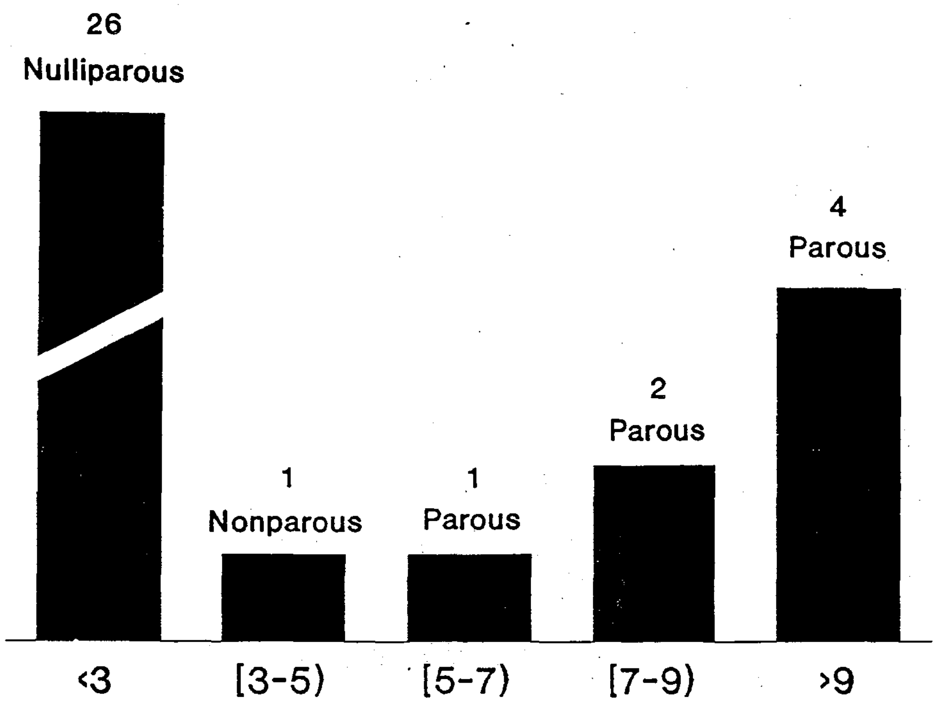


Fig. 12. Distribution of height (mm) for the largest teat on female fishers examined during suckling (8 May 1988, >9 mm, $\underline{n}$ = 1) and after weaning occurs in summer (10 Aug - 3 Dec, $\underline{n}$ = 33) in Waldo County, Maine, 1987-89. Parous and nonparous females ($\underline{n}$ = 8) were $\geq$2 yrs and had known reproductive histories via radiotelemetry; nulliparous females were <2 yrs ($\underline{n}$ = 15 measurements from radio-collared fishers [12 individuals] and 11 from carcasses). Sample sizes are above bars.

DISCUSSION

Fertility Rate

In both years, fertility rates based on PS (88% and 67% in 1988 and 1989, respectively) corresponded well to observed rates of natal denning (1988: 100%, *n* = 4 radio-collared females ≥2 yrs; and 1989: 67%, *n* = 3; Chapter 3). Fertility rates from Ontario, 1974-79 (M. A. Strickland, Ontario Minist. Nat. Res., pers. commun.) were similar to those from Maine (1988-89) in that BC were more prevalent that PS (Table 11), although Strickland (pers. commun.) questions the accuracy and consistency of counting darkened areas as PS. Although data from New Hampshire (1987) and Vermont (1988) (Crowley et al. 1990) were from 2 reproductive sequences (i.e., BC and PS from the same tract), they also showed higher counts of PS than BC, similar to fishers in Maine and Ontario (Table 11). Fertility rates based on PS from New Hampshire (Crowley et al. 1990) and Ontario (M. A. Strickland, pers. commun.) corresponded more closely to the average denning rate of 60% observed for fishers in Maine (Chapter 3) than did fertility rates based on BC (Table 11).

Litter Size

Litter sizes based on PS were closer to observed litter size in the wild (2.0-2.2 kits; Chapter 3) than were litter sizes based on CL or BC (Table 9). Crowley et al. (1990)

Table 11. Proportion of females from 4 locations having blastocysts (BC) and placental scars (PS) during 1975-89. Data for BC in year "X" and PS in year "X+1" (a single reproductive sequence) are presented when data are available; otherwise, data for a single year are presented.

Location and year(s)	Fertility rate[a] BC (n)	PS (n)
Central Maine		
1988	0.83 (18)	-
1989	-	0.67 (12)
Algonquin Region, Ontario[b]		
1975-76	0.80 (44)	0.43 (37)
1976-77	0.83 (18)	0.33 (6)
1977-78	0.85 (41)	0.57 (7)
1978-79	-	0.77 (31)
New Hampshire[c]		
1987	0.90 (49)	0.48 (31)
Vermont[c]		
1988	0.83 (60)	0.22 (51)

[a]Proportion of females examined that had BC (age ≥1 yr) or PS (≥2 yrs), respectively.

[b]Data courtesy of M.A. Strickland; PS counted on interior of uterine horns without magnification.

[c]Data from Crowley et al. 1990 (same methods).

also reported smaller litter sizes based on PS (2.8 and 2.5) than for CL (3.7, n = 50 and 3.6, n = 60) or BC (3.2 and 2.0) in New Hampshire and Vermont, respectively (Table 11).

Fecundity Rate

Crowley et al. (1990) found that modal and median litter size in fertile females were 3-4 for all indices but dropped to 0 for PS when all females were considered. They suggested that per capita litter size at birth is affected more by a drop in fertility rate between formation of BC and implantation (i.e., loss of entire litter) than by a drop in litter size (i.e., partial loss of litter). Mean litter sizes based on PS in fertile females in Maine (2.3-2.9 [Table 9]; 2.9, n = 27 [Coulter 1966:78]) were similar to corresponding litter sizes from New Hampshire and Vermont (2.8 and 2.5, respectively); all litter sizes based on PS were more similar to litter size in wild fishers from Maine (2.0-2.2 kits per female in the natal den, 1988-89; Chapter 3) than were litter sizes based on CL or BC.

Prenatal mortality for fishers that implant blastocysts evidently is low; combined samples of CL and embryos from the same females (Wright and Coulter 1967:74-75, n = 8 females; Leonard 1986:36, n = 3; Douglas and Strickland 1987:514, n = 45) showed 175 embryos for 182 CL, only a 4% intrauterine loss. The physiological cost of active gestation may have caused selection for fishers that either implant all or no BC. Relatively few females may implant blastocysts and then resorb or abort some of their fetuses, although entire litters may be lost soon after implantation and not leave PS (cf. Conaway 1955, Sanderson and Nalbandov 1973:65).

PS counts in mink (Mustela vison) with known reproductive histories were contradictory: Elder (1952) found scars during December in only 8 of 100 females known to have whelped the previous spring, whereas Larson (1967) suggested that counts of PS (n = 236 females with known litter sizes) are valid for mean litter size in a population but not for litter size of individuals. Counts of PS were less than known litter sizes for 67 females (28%), but Larson (1967:21) did not mention any instances of no scars for a female known to have whelped kits.

Visibility and persistence of PS seems to vary by taxonomic group, likely reflecting anatomical and physiological differences. PS in rodents are readily seen and persist for >1 reproductive season in many species, similar to canids, felids, and raccoons (Payne 1982, Gilbert 1987). Rodent placentas tend to have a lesser separation of maternal and fetal blood supplies than do placentas in carnivores (Gunderson 1976), so the bleeding associated with parturition is probably greater for rodents. Visibility and persistence of PS within Carnivora may also correspond to timing of parturition and estrus. Changes might occur in the endometrium (Wood 1955, Kordek and Lindzey 1980), and the macrophages forming the PS might migrate (Martin et al. 1976) or be obscured with the onset of estrus. Because fishers mate <2 weeks after parturition (Hall 1942, Powell 1982), the rapid changes in the reproductive tract might lessen visibility of PS relative to those in other delayed implanters, but there have been no tests to verify that scars fade prior to autumn. Crowley et al. (1990) suggested that postmortem degeneration of tracts (i.e., darkening, desiccation) did not affect counts of PS in December.

Counts of PS were obtained more rapidly and may be a better index to both fertility rate and litter size in wild fishers than counts of CL or BC, but some discrepancies may occur because PS may form from resorbed or aborted fetuses (Payne 1982). Species having >1 embryo in a litter commonly resorb fetal mortalities instead of aborting the litter, but fetal membranes may survive or late-term embryos become mummified until being expelled at full term (Brambell 1948, Hafez 1974:365). Scars of resorbed fetuses may be indistinguishable from scars of parturition (Osborn 1953, Davis and Emlen 1948), particularly after a period of development (Conaway 1955, Sanderson and Nalbandov 1973). However, persistence of PS for >1 reproductive sequence in fishers is unlikely.

Scar formation and persistence should be studied in fishers with known litter sizes. Laparotomies could allow periodic viewing of implantation sites and development of young (Jonkel and Weckwerth 1963, Sanderson and Nalbandov 1973), including nulliparous adults for controls (cf. Conaway 1955) and marking of implantation sites for later scrutiny (Larson 1967). Information on histological changes, particularly migration of macrophages (Martin et al. 1976), might explain the disappearance of PS when reproductive tracts are preserved or cleared (Wright and Coulter 1967, this study). Studies using controls and marked implantation sites are needed to test the validity of PS as an index to productivity.

MANAGEMENT IMPLICATIONS

Counts of hemorrhage sites, presumed to be PS, in the uterine horns of adult fishers were faster to obtain and corresponded better to observed litter sizes and rates of natal denning in the wild than did counts of CL or BC. However, formation and persistence of PS as a result of implantation and successful parturition, or whether PS anatomically correspond to implantation sites, is unknown for fishers.

Teat size on fisher pelts may be useful to estimate the proportion of adult females ≥2 yrs in a population, including the proportion of adults that suckled young the previous reproductive period. Teat size on parous and nonparous adult females seem to be sufficiently distinct to assign reproductive status to unknown individuals. If size distinctions exist during autumn and hold true after fishers are skinned and the pelts stretched and dried, a large sample of pelts could be examined at fur auctions because most auction houses currently prefer fisher pelts with the fur side out (Obbard 1987). Fisher pelts are tagged in most jurisdictions, so date and origin of capture would be known, and the pelt index could be validated by cross-referencing to age distributions determined from teeth of harvested animals. A potential problem with teats is observer bias in measuring soft anatomy.

Counts of PS and the proportion of adult females with enlarged teats may be useful as reproductive indices in fishers. If validated with direct estimates of reproduction, these indices might permit comparison among bioclimatic regions or with other harvest indices, such as juveniles per adult female (Douglas and Strickland 1987).

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Appendix A. Development of wild fisher kits in southcentral Maine.

ID[a]	Kit age (wks)[b]	Date handled	Length (cm)	Weight (g)	Eyes open	Teeth erupted[c]	Behavioral disposition
M250	6.5	4/27/89	32	340	left one	none	mewing, crying, clinging, crawling under cover
M254	6.5	4/27/89	33	410	neither	none	same
F255	6.5	4/27/89	34	390	neither	none	same
M397	6.5	5/10/88	44	705	both	U+L C, U I	same
F395[d]	6.5	5/10/88	42	610	both	same	same
M391	8.0	5/14/88	47	930	both	U+L C, U I + PM	mewing, clinging
M388	8.0	5/21/88	48	805	both	all	crawl rapidly on ground, climb awkwardly, slash at handlers
M389[e]	8.0	5/21/88	47	860	both	all	same
F386	8.0	5/21/88	48	710	both	all	same
M393	8.5	5/19/88	49	930	both	all	aggressive in defending den; slash and scream

[a]M = male, F = female.

[b]Time since suspected birth of kits on the estimated first day of denning.

[c]U = upper, L = lower, C = canines, I = incisors, and PM = premolar.

[d]F401's kit; presumed to be F211 (see Chapter II).

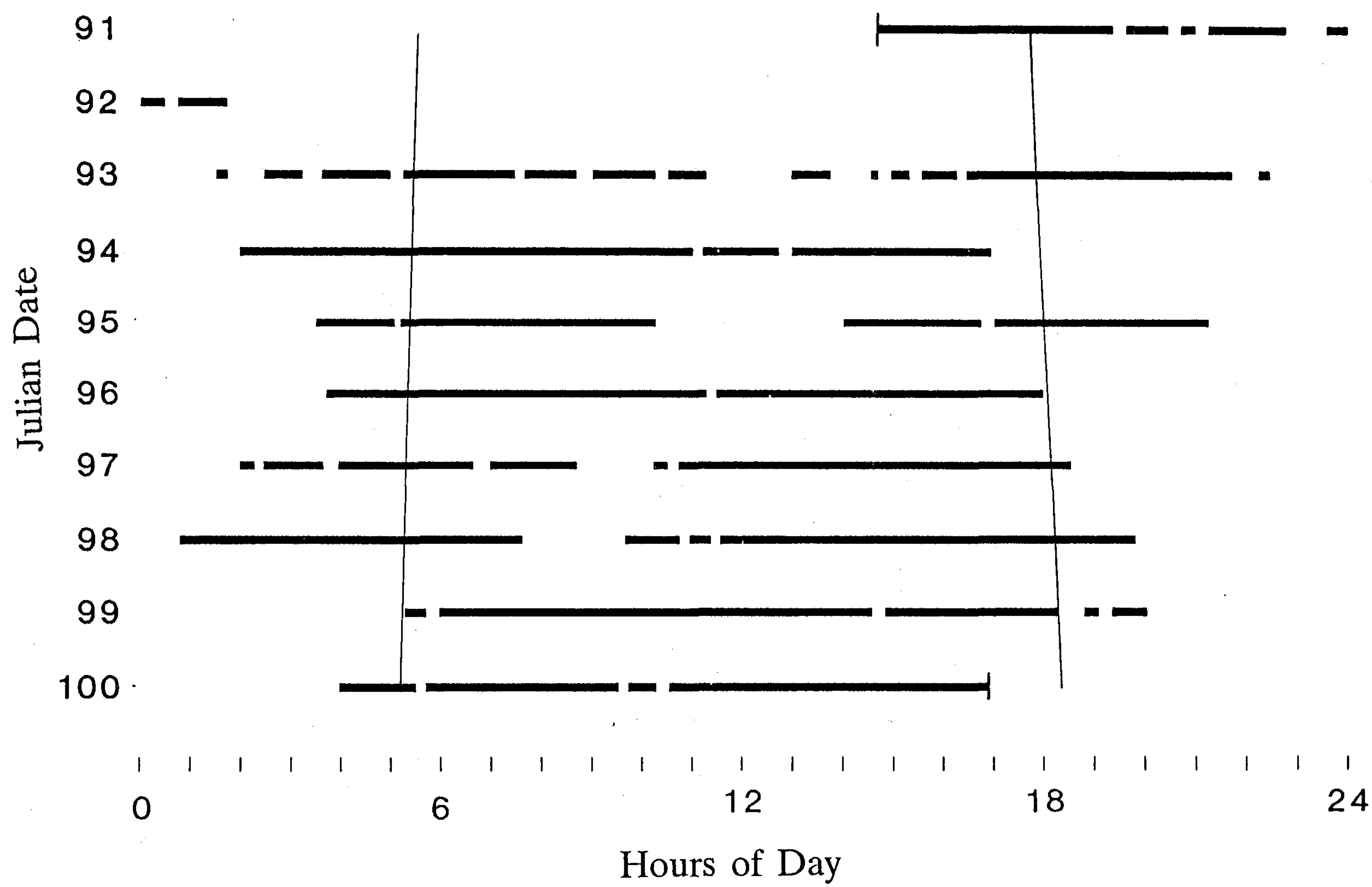
[e]F325's kit; presumed to be M206 (see Chapter II).

Appendix B. Measurements of tree and cavity size for natal dens used by fishers in Waldo County, Maine, 1986-89.

Species	DBH (cm)	Entrance height (m)	Entrance size (cm)	Cavity volume (m^3)[a]
aspen	30	7	10x10	-
aspen	50	5	8x8	-
aspen	40	3	8x10	-
aspen	45	12	8x15	-
aspen	60	11	10x10	-
aspen	45	8	-	-
aspen	75	5	20x25	-
aspen	35	8	7x10	-
aspen	50	8.9	8x9	0.06
aspen	30	12	9x10	0.25
aspen	45	4.7	7x13	0.28
aspen	25	10	-	-
aspen	45	11	-	-
aspen	43	5.3	8x16	0.02
aspen	38	0.9	7x18	0.02
aspen	45	1.3	8x15	0.02
basswood	45	9	10x15	0.08
basswood	60	6.3	9x15	0.43
birch	92	3	10x14	0.07
birch	48	4.4	8x10	-
elm	75	-	-	-
elm	75	-	-	-
hemlock	60	9.2	11x15	0.08
red maple	45	4.5	10x15	0.12
red maple	25	4.6	-	0.57
red maple	36	-	8x15	0.37
sugar maple	60	3	-	-
sugar maple	75	7.5	-	-
oak	90	8	15x20	-
oak	60	6.3	9x15	0.43
white pine	40	10.5	-	-

[a]Cavity volume below lip of entrance; only measured when cavity was well-defined.

Appendix C. Continuous monitoring of female fisher F459 at initial natal den, 1-10 April 1986. Vertical axis is Julian date; kit(s) were born ca. day 71. Presence within 15 m of den was noted by 15 min interval and represented by solid lines, with breaks in monitoring denoted by vertical lines. Sunrise and sunset are drawn across all days. Monitoring was terminated 10 April because of equipment failure.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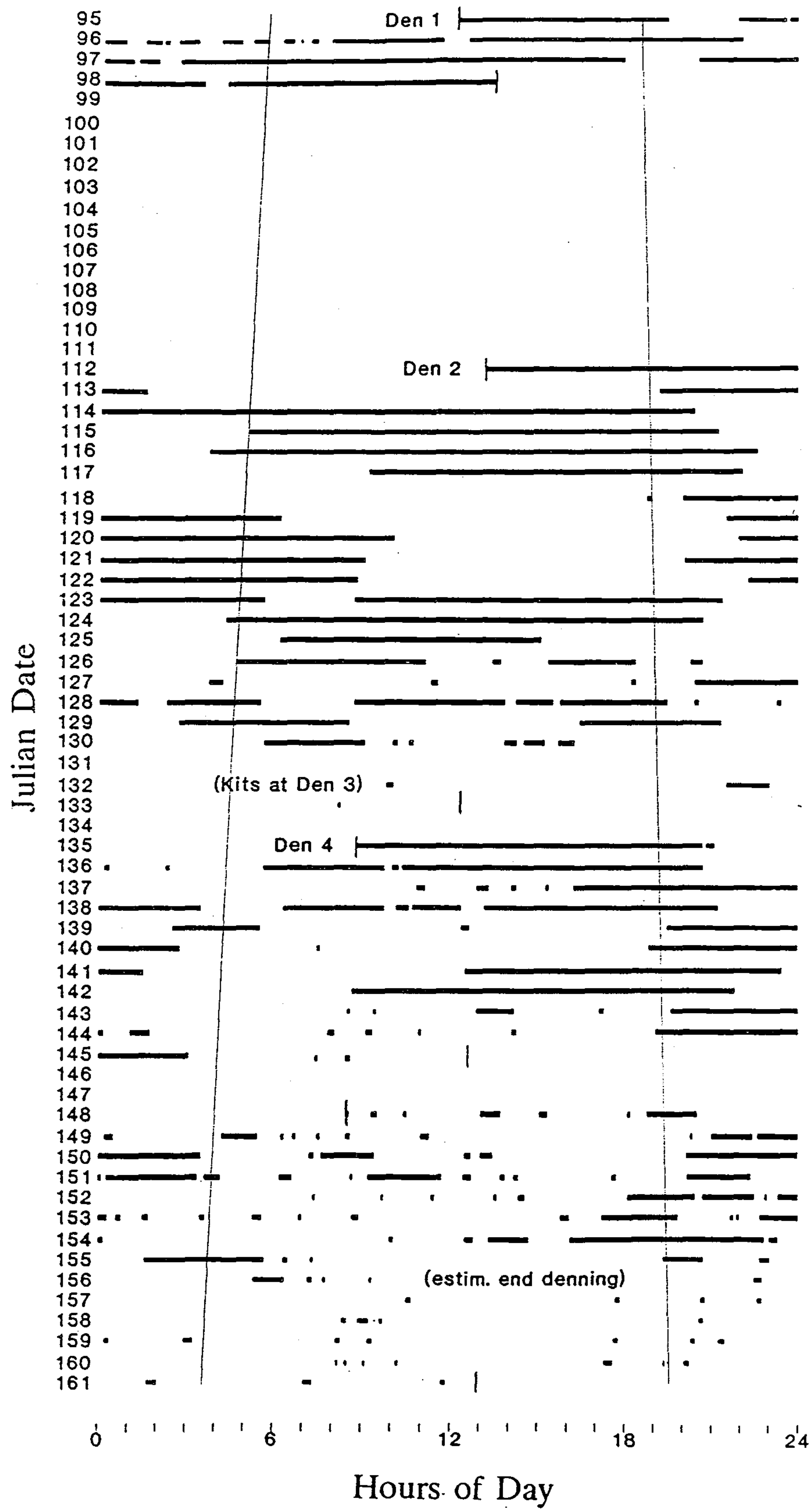
97
98
99
100
Julian Date
0
6
12
18
24
Hours of Day

Appendix D. Continuous monitoring of female fisher F401 at 3 natal dens, 4 April - 9 June 1988. Vertical axis is Julian date (+1 for leap year); 2 kits born ca. day 73. Presence within 15 m of den is represented by solid lines, with breaks in monitoring denoted by vertical lines. Sunrise and sunset are drawn across all days.



Den 1
Den 2
(Kits at Den 3)
Den 4
(estim. end denning)
Julian Date
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96
97
98
99
100
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103
104
105
106
107
108
109
110
111
112
113
114
115
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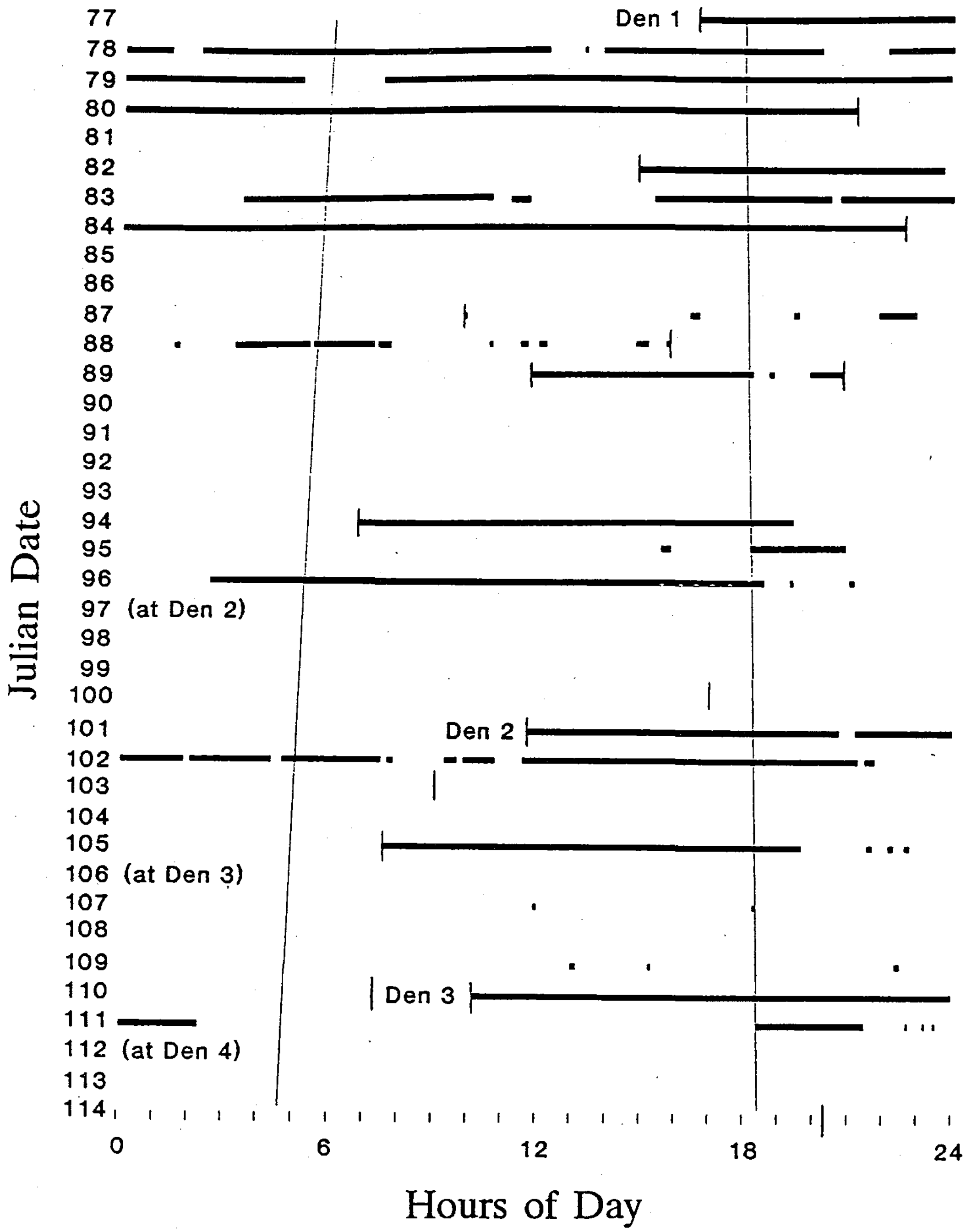
152
153
154
155
156
157
158
159
160
161
0
6
12
18
24
Hours of Day

Appendix E. Continuous monitoring of female fisher F460 at 3 natal dens, 18 March - 24 April 1989. Vertical axis is Julian date; 3 kits were born ca. day 71. Presence within 15 m of den is represented by solid lines, with breaks in monitoring denoted by vertical lines. Sunrise and sunset are drawn across all days.



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92
93
94
95
96
97 (at Den 2)
98
99
100
101
102
103
104
105
106 (at Den 3)
107
108
109
110
111
112 (at Den 4)
113
114
Den 1
Den 2
Den 3
0
6
12
18
24
Julian Date
Hours of Day

Appendix F. Food habits of 4 fisher families in Waldo County, Maine, 1988.

The ground below tree cavities used as resting sites by fisher families (mothers and kits) sometimes was littered with scats and remains of prey, including a juvenile raptor, fledgling bluejays (*Cyanocitta cristata*) and northern flickers (*Colaptes auratus*), young snowshoe hares (*Lepus americanus*), and red squirrels (*Tamiasciurus hudsonicus*). Defecation by three kits was observed, and scats were collected: one contained snowshoe hare (21 May); a second contained vole (*Clethrionomys* or *Microtus*) (6 Jun); and a third contained snowshoe hare, vole, and the fruit from common winterberry holly (*Ilex verticillata*) (25 Sep).

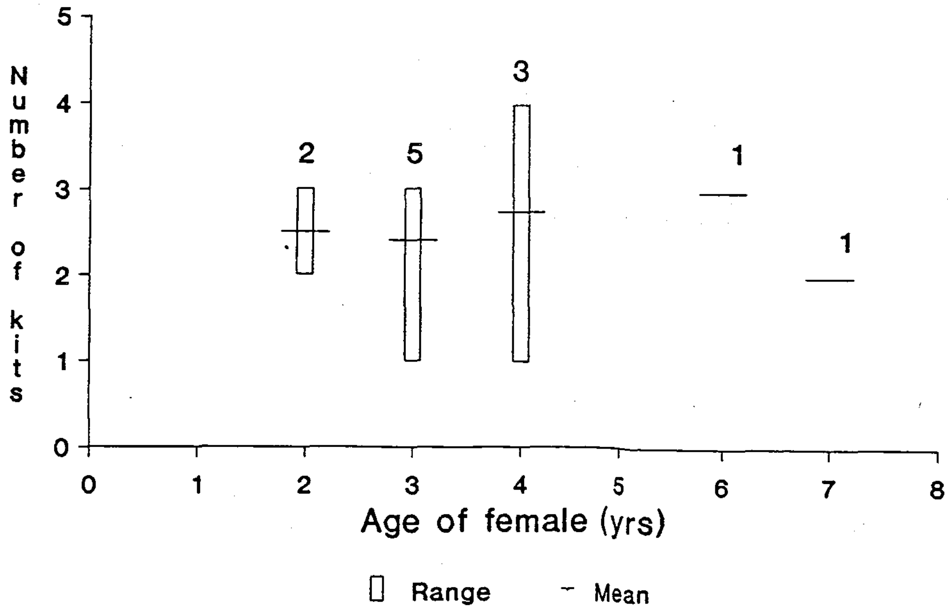
Appendix G. Reproductive histories of 12 female fishers radio-collared for 25 fisher-seasons (season = March-June) in Waldo Co., Maine, 1984-1989. N = did not den, Y = did den [litter size], L = lactating when captured in mid April but did not den afterwards, J = juvenile during previous mating season, ? = female not collared during entire female-year and reproductive success based on whether mammillae were enlarged on subsequent recaptures.

ID	1984[a]	1985[a]	1986[a]	1987[a]	1988	1989	birthdate
1112	N J	N	-	-	-	-	1982 (1983?)
444	-	N	-	-	-	-	1983
325	-	N	Y	Y	Y(3)	-	1982
450	-	N	-	-	-	-	1981
401	-	L	N	Y	Y(2)[b]	N	1981 (1982?)
414	-	J	-	-	Y(1)	-	1984
430	-	Y?	N?	N	-	-	1980
448	-	-	Y	-	-	-	1981
459	-	-	Y	-	-	-	1984
460	-	-	J	N	Y(1)	Y(3)	1985 (1984?)
461	-	-	L	Y	-	-	1979 (1980?)
244	-	-	-	-	-	Y(?)	unknown

per Randy Cross Jan. 1991

[a]Modified from Arthur and Krohn (1990).

[b]F211, female kit of F401 in 1988, produced 1st litter as 2-yr-old in 1990.



Appendix H. Litter size by age of female for 5 wild (Table 1) and 7 captive (Hall 1942:146) litters of fishers.

Appendix I. Tag loss and recovery of ear-tagged fishers kits in Waldo County, Maine, 1988 and 1989.

One kit had an ear tag placed in 1 ear, and 9 kits had tags placed in both ears. Of 6 kits recovered 3-6 months after eartagging, 2 had lost their tags (from 1 and 2 ears, respectively) by 4 months after tagging. Of the 4 captured with ear tags, 3 had both tags intact and 1 had a single tag intact. One kit had both ear tags intact 10 months after tagging.

One kit from each litter in 1988 was captured and radiocollared in the home range of its mother between August and October 1988. One male kit had both ear tags present, and a male and female kit had ripped ears where tags were placed. A juvenile female without either torn ears or ear tags was caught and remained within F460's home range until late January 1989; as mentioned in Chapter 3, I assumed it was a kit of F460 that I had missed during the den visit in May. During the fur trapping season (30 Oct-4 Dec), another kit with ear tags was trapped.

Appendix J. Interval survival that composes the annual or average annual survival for age-sex classes of fishers in Waldo County, Maine (JF = juvenile females, age 7.5-12 months; J = all juveniles; AF = adult females, age ≥12 months).

	Nontrapping (323-329 d)[a]					Trapping (36-42 d)				
Class	n[b]	D[c]	RD[d]	Rate	95% CL	n	D	RD	Rate	95% CL
JF 1984-89	5	1	296	0.72	[0.37,1.0]	13	7	291	0.39	[0.19,0.78]
J 1984-89	16	2	1178	0.85	[0.65,1.0]	39	22	927	0.39	[0.26,0.58]
AF 1984	1	0	174	1.0		1	0	38	1.0	
AF 1985	9	1	1250	0.77	[0.46,1.0]	8	2	206	0.69	[0.41,1.0]
AF 1986	9	0	1407	1.0		7	0	190	1.0	
AF 1987	7	0	1931	1.0		5	1	220	0.83	[0.57,1.0]
AF 1988	7	1	1404	0.79	[0.50,1.0]	5	1	162	0.80	[0.52,1.0]
AF 1989	7	1	1337	0.79	[0.49,1.0]	3	1	68	0.54	[0.16,1.0]
AF 1984-89	39	3	7503	0.88	[0.78,1.0]	30	5	884	0.80	[0.66,0.97]

[a]Juvenile estimates were calculated based on a nontrapping interval from the end of trapping season (late Dec) to 15 March ($\bar{x}$ = 99 d, range 95-101 d).

[b]Number of radio-collared fishers monitored during at least part of the interval.

[c]D = deaths.

[d]RD = radio-days.

Appendix K. Estimating summer survival of fisher kits via observations in Waldo County, Maine, 1988.

Mothers and kits were observed after denning (mid June onward) by quietly stalking them when the transmitter signals were steady, indicating a resting animal. Individual kits could not be identified, but litter size could be estimated.

Kits were seen on 9 of 49 attempts to observe 4 fisher families starting in mid June 1988 (postweaning). On 31 attempts the females were not seen because they became active (22) or were in a tree cavity (6) or burrow (3). Females were observed alone on 9 occasions, often in or near tree cavities; kits may have been present but hidden from view.

Litter sizes are given in Appendix G. F325 was observed once with 1 kit, and 2 of her kits were observed after she left a temporary den immediately before an observer arrived; F401 was never seen with kits; F414 was seen once with her kit; and F460 was observed 6 times with 1 kit. Attempts to stalk the fisher families ceased in early August because thick vegetation made stalking difficult.

Appendix L. Tetracycline as a biomarker in fisher kits.

In 1989 I injected approximately 375 mg/kg body weight of oxytetracycline hydrochloride (Medamyrin, Tech America, Kansas City, MO) subcutaneously in the flank of 3 kits to determine if teeth recovered in the future would have a fluorescing biomark (Ellenton and Johnston 1979) useful for identification if the ear tags were lost. The carcass of a marked kit (2 ear tags) was recovered by a trapper, and a canine was sectioned to ca. 10 um and mounted on a glass slide using Elvanol. Slides were viewed under a 400X light microscope using a 390 nm exciter and 530 nm barrier filter (C. E. Rupprecht, Wistar Institute, Philadelphia, U.S.A., pers. commun.).

A golden-yellow fluorescence at 640 nm was seen in the canine taken from a kit 7 months after injection with tetracycline. Unmarked teeth used as controls did not fluoresce (C. E. Rupprecht, pers. commun.).

Tetracycline provides a positive mark to verify kits suspected of having lost ear tags. Teeth should be cleaned manually and stored at $\leq$-20°C in the dark until sectioned; do not boil, decalcify, or stain them (C. E. Rupprecht, pers. commun.).

BIOGRAPHY OF THE AUTHOR

Thomas Frederick Paragi was born on 19 March 1964 in New Hartford, New York. He attended Westmoreland Central School, graduating in June 1982. He began attending the State University of New York Agricultural and Technical College at Cobleskill in August 1982 and received an A.S. degree in liberal arts, with high honors, in May 1984. Tom attended the University of Washington in Seattle from June to December 1984 before transferring to the University of Alaska-Fairbanks, where he received a B.S. degree in Wildlife Management, magna cum laude, in May 1987.

In 1984-85, Tom worked for a fisheries consultant in Washington State and the U.S. Forest Service in Alaska, primarily on salmonids. He then worked for the U.S. Forest Service and the Alaska Cooperative Wildlife Research Unit on several projects with ungulates and waterfowl in Alaska. He has been a member of the Wildlife Management Institute and The Wildlife Society since 1985.

Tom entered the Graduate School of the University of Maine at Orono in February 1988 and served as a research assistant in the Maine Cooperative Fish and Wildlife Research Unit. He is a candidate for the degree of Master of Science in Wildlife Management in August 1990.