Chapter 13

Ecology of Canada Lynx in Southern Boreal Forests

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Abstract—Canada lynx occur throughout boreal forests of North America, but ecological conditions in southern regions differ in many respects from those in Canada and Alaska. To evaluate the extent to which lynx ecology and population biology may differ between these regions, we review existing information from southern boreal forests and compare our findings to information presented in Chapter 9 on lynx in the taiga. Throughout North America, lynx diets in both winter and summer are dominated by snowshoe hares. In southern boreal forests, alternative prey, especially red squirrels, are important constituents of the diet. This reliance on alternative prey may reflect a response to low-density hare populations in southern regions, because alternative prey are also important in the taiga during lows in the snowshoe hare cycle. In addition, limited information on lynx diets during snow-free months indicates that alternative prey are important during summer in both northern and southern populations, regardless of the status of local hare populations. As in the taiga, lynx in southern regions are associated with boreal and sub-boreal forest conditions, including upper elevation, coniferous forests in

the western mountains and mixed coniferous-deciduous forests in the Northeast. Throughout their range, lynx are absent or uncommon in dense, wet forests along the Pacific coast. In both northern and southern regions, lynx occur predominantly in habitats where snowshoe hares are abundant, especially early successional stands with high stem densities. However, in southern boreal forests, such habitats appear to be used primarily for hunting; all known den sites in southern regions were located in mature forest stands with large woody debris. As in the taiga during times of hare scarcity, relatively large home ranges appear to be characteristic of lynx in southern boreal forests. Lynx dispersal movements are similar to those reported from the taiga. However, only lynx in southern forests are known to make exploratory movements prior to dispersal. We speculate that such explorations may reflect a more heterogeneous habitat mosaic, and a correspondingly lower probability of successful dispersal in southern regions. Demographic characteristics of southern lynx populations, including low densities, low pregnancy rates, low litter sizes, and high kitten mortality rates are similar to those reported from the taiga during times of hare scarcity. As in the taiga, we found little evidence that roads represented a significant disturbance or mortality factor for lynx. Roads into lynx habitat may, however, provide access to generalist competitors, such as coyotes and bobcats. Although there is little evidence that competition with other predators negatively influences lynx populations, this aspect of their ecology has not been studied in southern boreal forests. In summary, differences in lynx ecology between populations in southern boreal forests and those in the taiga appear to be related primarily to the use of alternative prey species; the effect of habitat patchiness on movements, reproduction, and survival; and the potential effects of different communities of predators and competitors on lynx populations.

Introduction

Canada lynx occur in most boreal forest habitats in North America, including the classic boreal forests or taiga of northern Canada and Alaska, upper elevation coniferous forests of the Rocky Mountains and Cascade Range, and mixed coniferous-deciduous forests of southeastern Canada, New England, and the Great Lakes states (Chapters 3 and 8; McCord and Cardoza 1984; Quinn and Parker 1987). Most of the geographic range of lynx in North America occurs in the taiga, however, where Canada lynx ecology has been studied in greatest detail (Chapter 9). Lynx reach their highest densities in the taiga, where populations undergo dramatic 10-year cycles in delayed synchrony with snowshoe hare populations (Elton and Nicholson 1942; Keith 1963; Chapter 9).

Some authors have argued that lynx populations in the southern portion of their range in the contiguous United States do not cycle in abundance, but occur at relatively stable densities comparable to those found during cyclic lows in the taiga (Keith 1963; Koehler and Aubry 1994). This hypothesis is based largely on the observation that snowshoe hare populations in the southern portions of their range are either stable or have cycles of very low amplitude (Adams 1959; Keith 1963; Dolbeer and Clark 1975; Wolff 1980, 1982). However, Hodges (Chapter 7) has compiled new information on snowshoe hare populations in southern boreal forests that indicates that hares may fluctuate in number more than previously thought, but at much lower amplitudes than those recorded in the taiga. Ecological conditions in southern boreal forests occupied by lynx differ in many ways from those in the taiga (Chapter 3). Thus, the ecology of lynx in southern boreal forests may differ in important ways from that described for populations in the North (see also Chapter 5). If so, such differences would have important implications for lynx conservation in the contiguous United States.

In this chapter, we review existing information on lynx ecology in boreal forests south of the Polar ecoregions (Bailey 1998) and compare and contrast these findings to those presented in Chapter 9 on lynx ecology in northern boreal forests. Information considered here includes all studies of lynx ecology in the contiguous United States, as well as those conducted in Humid Temperate and Dry ecoregions in the southern Canadian Rocky Mountains (Chapter 12) and on Cape Breton Island in Nova Scotia (Parker 1981; Parker et al. 1983).

Food Habits and Relationships With Prey

Throughout North America, the distribution of lynx is virtually coincident with the distribution of snowshoe hares (McCord and Cardoza 1984; Bittner and Rongstad 1984) and, within that range, lynx tend to occur in habitats where snowshoe hares are most abundant (Koehler and Aubry 1994; Chapter 9). In northern regions, lynx prey almost exclusively on snowshoe hares during winter; however, during snow-free seasons or when hares are at low abundances, alternative prey, especially red squirrels, are taken in higher proportions (Chapter 9). Although limited information from studies in the western mountains indicates a similar predominance of snowshoe hares in the diet of lynx (Koehler and Aubry 1994), hare densities are typically low in southern boreal forests compared to northern regions (Chapters 6 and 7).

There have been few studies of lynx food habits in southern boreal forests (Table 13.1). Among 29 lynx scats collected in north-central Washington during winter and summer from 1985 to 1987, 23 (79%) contained snowshoe

Table 13.1—Frequency of occurrence (%) of prey items in diets of Canada lynx in North America. Contents of scats, stomachs, and digestive tracts may contain more than one prey item; thus, total percentages for these analyses may exceed 100%.

Study area	Snowshoe hare	Red squirrel	Other small mammals	Grouse and ptarmigan	Other birds	Ungulates	Other
Southern boreal forests							
North-central Washington; annual (n = 29 scats)[a]	79	24	3			7	
Southern Canadian Rocky Mountains; winter (n = 137 kills found during snow tracking)[b]	52	30	8	3	1		6
Cape Breton Island, Nova Scotia; winter (n = 75 stomachs)[c]	97	1	3	3		5	
Cape Breton Island, Nova Scotia; winter (n = 55 scats)[c]	93		7	4	2	5	
Cape Breton Island, Nova Scotia; summer (n = 441 scats)[c]	70	4	4-5	1	6-7	9	<1
Northern boreal forests during low snowshoe hare densities							
Central Alberta; winter (n = 338 items found in stomachs)[d]	35	12	33	6	6	3	7
Central Alberta; winter (n = 54 kills found during snow tracking)[e]	56	7		15			22
Southwestern Yukon; winter (n = 280 kills found during snow tracking)[f]	20	64	13	1			1
Southwestern Yukon; winter (n = 101 scats)[f]	79	50	21				7
Kenai Peninsula, Alaska; winter (n = 161 scats)[g]	91	15	13	10	1	7	6
Kenai Peninsula, Alaska; winter (n = 16 kills found during snow tracking)[g]	63	19	13	6			
Kenai Peninsula, Alaska; summer (n = 42 scats)[g]	67	50	29	12	10		10
Northern boreal forests during high snowshoe hare densities							
Central Alberta; winter (n = 72 items found in stomachs)[d]	90		5		3		1
Central Alberta; winter (n = 35 kills found during snow tracking)[e]	86	3		6			6
Southwestern Yukon; winter (n = 222 kills found during snow tracking)[f]	89	3	3	4			1
Southwestern Yukon; winter (n = 239 scats)[f]	92	5	16				20
Kenai Peninsula, Alaska; winter (n = 41 scats)[h]	100	5	7		10		
Alberta and Northwest Territories; winter (n = 52 digestive tracts)[i]	79	2	10	10	13	12	2
Alberta and Northwest Territories; summer (n = 23 digestive tracts)[i]	52	9	39	8	26		

[a]Koehler 1990; [b]Apps Chapter 12; [c]Parker et al. 1983; [d]Brand and Keith 1979; [e]Brand et al. 1976; [f]O'Donoghue et al. 1998 (data on frequency of occurrence in scats provided by M. O'Donoghue); [g]Staples 1995, unpublished; [h]Kesterson 1988, unpublished; [i]van Zyll de Jong 1966

hare and seven (24%) contained red squirrels; remains of both species were also found at den sites (Koehler 1990). Using Koehler's (1990) pellet plot data, Hodges (Chapter 7) estimated fall snowshoe hare densities on the study area at 0.09-1.79 hares/ha. Snow tracking along 20.5 km of lynx trails detected eight chases of prey by lynx; snowshoe hares were chased six times and captured twice, whereas red squirrels were unsuccessfully chased twice. Lynx had been observed capturing red squirrels in the study area previously, however (Brittell et al. 1989, unpublished). Other prey items, including remains of a deer fawn, adult deer, and white-footed mouse, were each found in only one scat.

During snow-tracking studies from 1996 to 1998, Apps (Chapter 12) documented 137 lynx kills during winter in the southern Canadian Rocky Mountains. Prey species included 71 (52%) snowshoe hares, 41 (30%) red squirrels, nine (5%) northern flying squirrels, five (3%) martens, voles, and grouse, one northern flicker, and five "unknown." Snowshoe hare densities in the study area were estimated at 0.01-0.47 hares/ha. A radio-marked male lynx scavenged a road-killed mule deer for several days before being driven off by wolves. The only food habits information collected during snow-free months was the observation that a radio-marked juvenile male hunted meadow voles on seven occasions. There are several reported observations of lynx hunting ground squirrels in southern boreal forests. In Wyoming, a male lynx was seen hunting Wyoming ground squirrels in sagebrush habitat in late April, and a female was observed hunting similarly in early July (Chapter 11). Barash (1971) observed two adult and one juvenile lynx cooperatively hunting Columbian ground squirrels during summer in Glacier National Park, Montana.

In contrast to findings from western montane regions, studies in Nova Scotia (Parker 1981; Parker et al. 1983) indicated that alternative prey were relatively unimportant in lynx diets during winter. However, snowshoe hares occurred in the study area at densities higher than most recorded in the taiga (5.8-10 hares/ha; see Chapter 6), suggesting that food habits of lynx in Nova Scotia may not be comparable to those of other lynx populations in southern boreal forests, where hares occur at substantially lower densities (Chapter 7). In addition, although southern red-backed voles, masked shrews, ruffed grouse, and spruce grouse were all considered to be common in the study area, red squirrels were relatively rare. In "advanced" successional stages (16-30 years after cutting), hare densities declined from 10 hares/ha in 1977 to 1.7 hares/ha in 1979. Nevertheless, for all years combined, snowshoe hares were present in 97% of stomachs examined ($n = 75$) and 93% of scats ($n = 55$) collected during winter; red squirrels were found in only one stomach (Parker et al. 1983). Among 200 chases detected during

snow tracking in the winter of 1977-1978, 198 were of snowshoe hares that resulted in 34 kills; the remaining two chases were of ruffed grouse (Parker 1981). During summer, however, alternative prey were more important in the diet; only 70% of scats examined ($n = 441$) contained remains of snowshoe hare. Other foods of lynx during summer included birds, small mammals, and carrion.

Very few studies of lynx food habits during snow-free periods have been conducted in North America (Table 13.1; Chapter 9). Based on available information, however, there appear to be few essential differences in the food habits of the lynx throughout its range. Regardless of geographic location, lynx diets are dominated by snowshoe hares during all seasons of the year. If hares are abundant, lynx subsist almost exclusively on them during winter. In the taiga, alternative prey are important in the winter during lows in the snowshoe hare cycle (Table 13.1; Chapter 9). During summer in northern boreal forests, alternative prey are more abundant in lynx diets regardless of the status of local snowshoe hare populations (Table 13.1). It is unclear, however, whether this shift is related to increased availability of alternative prey or to decreased hunting success on hares during snow-free periods (Chapter 9). Although data are scarce, the red squirrel appears to be the most important alternative prey species throughout the range of lynx, with grouse, small mammals, and carrion of lesser importance in the diet. In southern boreal forests, limited data suggest that because snowshoe hares typically occur at low densities (Chapter 7), alternative prey may always be important components of lynx diets, especially in the western mountains.

Habitat Relationships

Historical and current records show that lynx occur primarily within Douglas-fir, spruce-fir, and fir-hemlock forests at elevations ranging from 1,500 to 2,000 m in the western mountains, boreal forest types at 250-500 m in the Great Lakes region, and mixed forest-coniferous forest-high tundra vegetation types at 250-750 m in the northeastern United States (Chapter 8). However, lynx habitat relationships within these forest types have been studied in only a few locations. Studies that documented habitat use with radiotelemetry have monitored relatively few animals: three lynx in Nova Scotia (Parker et al. 1983), five and two in Montana (Smith 1984, unpublished; Koehler et al. 1979, respectively), and seven in Washington (Koehler 1990). Brittell et al. (1989, unpublished) reported forest cover type and topographic attributes for home range areas of 23 radio-marked lynx in Washington, but such analyses do not provide reliable information on habitat selection. However, McKelvey et al.'s (Chapter 10) reanalysis of telemetry data from

Washington (Brittell et al. 1989, unpublished; Koehler 1990) has provided new information on selection of forest habitats and topographic features by lynx in that region. Intensive snow-tracking studies comparing habitat use with availability have only been conducted in Nova Scotia (Parker 1981; 192 km of trails).

Associations With Forest Types

In the western mountains, Canada lynx occur predominantly within boreal forests (Chapter 8; Koehler and Aubry 1994); elevational zones for these forests vary with latitude, ranging from an average of about 1,400 m in Washington to 2,700 m in Colorado (Chapter 3). The lynx study area in the southern Canadian Rockies (Chapter 12) is dominated by Engelmann spruce-white spruce and subalpine fir forests occurring at elevations between 1,200 and 3,000 m; lodgepole pine is present as a seral species. The area where lynx are being studied in western Montana (Chapter 11) ranges from 1,200 to 2,100 m in elevation and is dominated by Douglas-fir, western larch, and lodgepole pine at lower elevations, and subalpine fir, whitebark pine, and Engelmann spruce at upper elevations. Habitat used by five radio-marked lynx in Montana was described by Smith (1984, unpublished) as occurring within subalpine fir forest associations. The lynx study area in western Wyoming (Chapter 11) is located at 2,600-2,750 m in elevation, where pure stands of lodgepole pine occur on drier sites and spruce-fir is generally restricted to north-facing slopes; south-facing slopes are dominated by sagebrush and wheat grass communities. Halfpenny et al. (1989, unpublished) reported lynx above 2,700 m along edges of dense spruce-fir stands near parklands and aspen stands in Colorado.

Forest cover types selected by lynx in the Cascade Range of north-central Washington (Chapter 10) are similar to those used by lynx in the Rocky Mountains. In the Cascades, lynx selected lodgepole pine cover types at elevations ranging from 1,370 to 2,130 m. During winter, however, lynx shifted their activities to elevations below 1,520 m, avoiding those above 1,980 m. During summer, lynx selected northeast aspects, but whether lynx selected these sites for thermal or other features is not known (Chapter 10). Douglas-fir, ponderosa pine, and western larch stands were used less than expected by lynx.

Lynx are forest dwellers, but historical records (Chapter 8) and recent studies (Chapter 11) show that lynx occur occasionally in non-forested areas, such as shrub-steppe habitats in eastern Montana, Wyoming, and Idaho. However, such observations appear to represent either transient individuals or resident animals searching opportunistically for prey.

Associations of lynx occurrences and forest cover types in the Northeast described in Chapter 8 fit closely with published descriptions of lynx habitat. On Cape Breton Island in Nova Scotia, lynx occupied forested habitats at elevations from 360 to 390 m, where the climax vegetation consisted of balsam fir and black spruce bogs, and alder-bordered streams. Lynx also frequented open spruce-dominated bogs, where multiple tracks and evidence of play activity suggested that such sites may be used for resting and socializing (Parker 1981). Most trapping records from the White Mountains of New Hampshire during the 1960s were from elevations over 1,000 m in forest types dominated by hardwoods and spruce-balsam fir (Litvaitis et al. 1991). Brocke (1982) speculated that the historic distribution of lynx in the Adirondack Mountains of northern New York was associated with spruce-fir forest receiving heavy snowfall at elevations over 900 m. Descriptions of habitat used by lynx in the Great Lakes states are generally anecdotal in nature and provide few insights about lynx ecology in that region.

Forest types occupied by lynx in the taiga are described as boreal, subboreal, and montane forests containing snowshoe hares; lynx are absent or uncommon, however, in wet, coastal forests of western Canada and Alaska (Chapter 9). These descriptions of broad forest associations are similar to those reported from southern boreal forests. In the contiguous United States, the range of lynx is essentially coincident with the distribution of boreal forest in the western mountains and northeastern United States (Chapters 3 and 8; McCord and Cardoza 1984); as in Canada and Alaska, lynx are absent from the dense, wet forests along the Pacific coast.

Stand-Scale Habitat Associations

Habitat use by lynx at the stand scale has been studied with both snow tracking and radiotelemetry in many areas of the taiga (Chapter 9), but there are few studies of this kind in southern boreal forests. In Montana, Koehler et al. (1979) reported that 26 of 29 lynx locations for two radio-marked lynx were in densely stocked lodgepole pine stands where hares were abundant; the remainder were in Douglas-fir and western larch stands. Selection by lynx of dense lodgepole pine stands containing high numbers of snowshoe hares has also been demonstrated in north-central Washington (Koehler 1990). Lodgepole pine is a seral, fire-dependent species in boreal forests of the western mountains (Chapter 3) and appears to be preferred by lynx in northern portions of the Cascade Range and Rocky Mountains (Koehler et al. 1979; Koehler 1990; Chapter 10). Average fire frequency in the North Cascades of Washington is 109-137 years (Chapter 3); but within the 1,800 km^2 study area in north-central Washington, fires burned areas >2,500 ha (more than half of an average female's home range) at more frequent

intervals (late 1800s, 1929, 1972, and 1994; Okanogan National Forest, unpublished). However, whether the persistence of lynx populations in this area (Chapter 8) is related to relatively short fire-return intervals is not known. Differences in fire ecology between northern and southern boreal forests and resulting implications for management of lynx habitat are discussed in detail in Chapters 3 and 15.

Early successional forests appear to be important for lynx in Nova Scotia. Snow tracking (Parker 1981) and radiotelemetry (Parker et al. 1983) studies on Cape Breton Island indicated that lynx selected early (5-15 years old) and advanced (16-30 years old) successional forests, followed by open mature conifer and open black spruce bog habitat types. Closed mature forests (both conifer and mixed conifer-hardwood), open mature mixed forests, riparian alder swales, and frozen lakes were used less than expected. During summer, use of successional habitat decreased and use of mature conifer habitat increased (Parker et al. 1983).

Parker (1981) found that lynx most strongly selected advanced successional forests, where hares were most abundant. However, among other habitat types, he found no consistent correlation between habitat selection and the relative abundance of snowshoe hares. Mature, mixed conifer-hardwood forests with relatively high hare populations were selected against, whereas open, mature coniferous forests with relatively few hares were used more often than expected. Parker speculated that factors other than prey abundance may influence habitat selection by lynx and suggested that lynx use open mature conifer forests, where hares are relatively scarce, for cover and travel. Parker also speculated that lynx use early and advanced successional stages, where hares are abundant, for hunting.

Koehler and Brittell (1990) described similar habitat use in north-central Washington; snow tracking revealed that lynx generally traveled in straight, non-meandering paths in mature forest stands with sparse understory cover, indicating that lynx were using stands where hares were scarce but not actively hunting in them. Such forest conditions were identified as "travel habitat" that provided security cover when lynx move between foraging or den sites (Koehler and Brittell 1990). From snow tracking, Koehler (1990) found that lynx traveled the edges of meadows but only crossed meadows where openings were less than 100 m wide. During winter, lynx were also observed traveling through silviculturally thinned stands with 420-640 trees/ha (Koehler 1990). From these observations, Koehler and Brittell (1990) speculated that lynx avoid open areas where security cover is lacking but that 420-640 trees/ha could provide adequate travel cover; during snow-free periods, shrub habitats may also be used for travel by lynx.

Koehler (1990) located four maternal den sites used by two females in north-central Washington, all of which were located on north-facing slopes in mature (>250 years) forest stands with an overstory of spruce, subalpine fir, and lodgepole pine that contained an average of 40 logs/50 m. A maternal den in Wyoming was located in a mature subalpine fir stand that had relatively dense understory cover from large woody debris and saplings (Chapter 11).

In the taiga, lynx typically prefer forested stands containing the densest populations of snowshoe hares; such habitats are generally represented by older (>20 years) regenerating stands of both natural and human origin, or mature stands with a dense understory (Chapter 9). However, even if hares are abundant, lynx generally do not occur in forested stands with extremely dense understories or in shrub-dominated sites, probably because lynx cannot hunt effectively in such stands (Chapter 9). Tangles of blowdown in mature forests are used for den sites, but recent work in the Yukon demonstrates that lynx may den in younger, regenerating stands (30 years old) containing blowdown or structures that provide similar cover, such as roots and dense vegetation (Chapter 9). The critical habitat component for maternal dens appears to be understory structure that provides security and thermal cover for kittens. Suitable understory structures are generally found in unmanaged, mature forest stands, but may also occur in early successional forests where windthrow and snags are present.

Although lynx in southern boreal regions generally select forested stands having abundant snowshoe hare populations, they also occasionally use habitats with relatively low numbers of hares. In contrast to findings from the taiga, habitats used by lynx in the southern portion of their range may include those that are used primarily for traveling between foraging sites and others that are used primarily for hunting (Koehler and Brittell 1990; Parker 1981). Although these speculations are based on relatively few data, habitats that contain abundant snowshoe hare populations in southern boreal forests may be more patchy and disjunct in distribution (Dolbeer and Clark 1975; Wolff 1980, 1982), forcing lynx to travel among foraging patches to find adequate prey. Further research on habitat use relative to the abundance of snowshoe hares is needed to evaluate this hypothesis.

Spatial Organization

Home Range

Ten studies (Brainerd 1985, unpublished; Brittell et al. 1989, unpublished; Koehler et al. 1979; Koehler 1990; Mech 1980; Parker et al. 1983; Smith 1984, unpublished; Chapters 11 [two studies] and 12) have documented spatial

organization of resident lynx populations in southern regions using radio-telemetry, but most were short-duration studies involving relatively few individuals (n = 1-8; Table 13.2). Home range studies vary considerably in design, implementation, and analysis resulting in many potential sources of bias. These include differences in the sex, age, and reproductive status of study animals, the status of prey populations, season of study, duration of study, sample size, sampling technique, and analytical approach, among others. Consequently, comparisons among studies are problematic and results should be interpreted cautiously.

Table 13.2—Mean home range sizes of Canada lynx in North America.

Location	Mean home range size (km^2)	Calculation method and season	Source
Southern boreal forests			
Southern Canadian Rocky Mountains	277 ± 71[a] (male; n = 3) 135 ± 124 (female; n = 3)	95% Minimum Convex Polygon (MCP), annual	Chapter 12
North-central Washington	49 ± 25 (male; n = 8) 37 ± 26 (female; n = 7)	100% MCP, annual	Brittell et al. 1989, unpublished
North-central Washington	69 ± 28 (male; n = 5) 39 ± 2 (female; n = 2)	100% MCP, annual	Koehler 1990
North-central Montana	36 (male; n = 1)	100% MCP, March-October	Koehler et al. 1979
North-central Montana	133 (male and female; n = 4)	100% MCP, annual	Smith 1984, unpublished
North-central Montana	122 (male; n = 6) 43 (female; n = 3)	100% MCP, annual	Brainerd 1985, unpublished
North-central Montana	238 ± 99 (male; n = 4) 115 ± 50 (female; n = 2)	95% MCP, annual	Chapter 11
West-central Wyoming	90 (male; n = 1) 66 (female; n = 1)	95% MCP, winter	Chapter 11
West-central Wyoming	91 (male; n = 1) 68 (female; n = 1)	95% MCP, summer	Chapter 11
Northeastern Minnesota	194 (n = 2) 87 (n = 2)	100% MCP, annual	Mech 1980
Cape Breton Island, Nova Scotia	26 (male; n = 1) 32 (female; n = 1)	100% MCP[b], summer	Parker et al. 1983
Cape Breton Island, Nova Scotia	12 (male; n = 1) 19 (female; n = 1)	100% MCP[b], winter	Parker et al. 1983
Northern boreal forests during low snowshoe hare densities			
Southwestern Manitoba	221 (male; n = 1) 158 (female; n = 2)	100% MCP[b], annual	Carbyn and Patriquin 1983
South-central Northwest Territories	26 ± 5 (male; n = 8) 44 ± 14 (male; n = 2) 25 ± 5 (female; n = 8) 63 ± 28 (female; n = 2)	95% MCP, annual, 1991-92 95% MCP, annual, 1992-93 95% MCP, annual, 1991-92 95% MCP, annual, 1992-93	Poole 1994

(con.)

Table 13.2—(Con.)

Location	Mean home range size (km^2)	Calculation method and season	Source
South-central Yukon	119 ± 189 (male; n = 6)	95% MCP, annual, 1992-93	Slough and Mowat 1996
	266 ± 106 (male; n = 2)	95% MCP, annual, 1993-94	
	23 ± 7 (female; n = 10)	95% MCP, annual, 1992-93	
	507 ± 297 (female; n = 4)	95% MCP, annual, 1993-94	
Southwestern Yukon	28 ± 5 (male; n = 4)	95% MCP, annual, 1992-93	M. O'Donoghue, personal communication
	35 (male; n = 1)	95% MCP, annual, 1993-94	
	40 ± 11 (male; n = 2)	95% MCP, annual, 1994-95	
	24 ± 16 (female; n = 3)	95% MCP, annual, 1992-93	
	34 (female; n = 1)	95% MCP, annual, 1993-94	
	45 (female; n = 2)	95% MCP, annual, 1994-95	
Interior Alaska	160 ± 38 (male; n = 5)	95% MCP, annual, 1991-92	Perham 1995, unpublished
	183 ± 66 (male; n = 6)	95% MCP, annual, 1992-93	
	30 ± 9 (female; n = 3)	95% MCP, annual, 1991-92	
	47 ± 23 (female; n = 23)	95% MCP, annual, 1992-93	
Northern boreal forests during high snowshoe hare densities			
South-central Northwest Territories	36 ± 8 (male; n = 7)	95% MCP, annual, 1989-90	Poole 1994
	17 ± 2 (male; n = 13)	95% MCP, annual, 1990-91	
	21 ± 6 (female; n = 4)	95% MCP, annual, 1989-90	
	18 ± 3 (female; n = 10)	95% MCP, annual, 1990-91	
Southwestern Yukon	14 ± 1 (male; n = 2)	90% MCP, annual	Ward and Krebs 1985
	13 ± 7 (female; n = 2)		
South-central Yukon	48 ± 26 (male; n = 7)	95% MCP, annual, 1989-90	Slough and Mowat 1996
	44 ± 23 (male; n = 12)	95% MCP, annual, 1990-91	
	20 ± 9 (female; n = 4)	95% MCP, annual, 1989-90	
	13 ± 4 (female; n = 13)	95% MCP, annual, 1990-91	
Southwestern Yukon	24 ± 9 (male; n = 7)	95% MCP, annual, 1990-91	M. O'Donoghue, personal communication
	39 ± 51 (male; n = 7)	95% MCP, annual, 1991-92	
	17 ± 14 (female; n = 4)	95% MCP, annual, 1990-91	
	17 ± 7 (female; n = 4)	95% MCP, annual, 1991-92	
Kenai Peninsula, Alaska	225 ± 220 (male; n = 6)	100% MCP[b], annual	Kesterson 1988, unpublished
	107 ± 53 (female; n = 8)		

[a]Standard deviation, if available from source.
[b]Proportion of points used not specified; assumed to be 100%.

In general, lynx home ranges in southern boreal forests are large compared to those reported from the taiga during times of high snowshoe hare densities (Table 13.2). Using only annual home range estimates from studies with sample sizes ≥3 listed in Table 13.2, the average mean home range size for males is 151 km^2 in southern boreal forests, 103 km^2 in the taiga during low hare densities, and 62 km^2 in the taiga during high hare densities. The average mean home range size for females in southern boreal forests is 72 km^2, whereas in the taiga, it is 109 km^2 during hare population lows and 30 km^2 during hare highs.

Use of centrally located "core" home ranges, where activities were concentrated, was reported from north-central Washington and Nova Scotia (Brittell et al. 1989, unpublished; Parker et al. 1983). In most studies, males used vacated territories when a neighboring male died or emigrated, and male ranges overlapped extensively with those of one to three females (Brittell et al. 1989, unpublished; Koehler 1990; Parker et al. 1983; Chapter 11). In Montana, home ranges of juveniles overlapped those of adults regardless of sex (Brainerd 1985, unpublished) but, in Nova Scotia, the home range of a juvenile female was adjacent to those of an adult male and an adult female during both winter and summer (Parker et al. 1983). Although factors affecting the selection of home ranges at the landscape scale are largely unknown, home range boundaries in Washington generally occurred along ridges and major rivers (G. Koehler, unpublished); major highways may also define home range boundaries (Chapter 12).

Few studies have investigated seasonal changes in home range use, and results are inconsistent (Table 13.2). In Wyoming, home ranges for both the male and female lynx were similar in size during winter and summer. In Montana, Brainerd (1985, unpublished) suggested that summer home ranges were much smaller than annual home ranges for both males and females, and Smith (1984, unpublished) reported the largest home ranges during the spring breeding season. However, home ranges for both the male and female lynx studied in Nova Scotia were smaller during winter than in summer, and Koehler (1990) reported that lynx in north-central Washington occupied the same home ranges for two or more consecutive years.

As reported for lynx populations in the taiga (Chapter 9), estimated home range sizes for lynx in southern boreal forests vary substantially and appear to be determined by numerous factors. However, relatively large home ranges appear to be characteristic of southern lynx populations, especially in the western mountains (Table 13.2). Both male and female home ranges in southern boreal forests are comparable to those occurring in the taiga during times of hare scarcity, and are substantially larger than those reported from the taiga during high snowshoe hare densities. In the north, lynx maintain similar-sized home ranges during most phases of the hare cycle but will expand home ranges when hare populations decline to low levels (Chapter 9). In most southern boreal forests, reported hare densities are similar to those occurring during population lows in the north (Chapters 6 and 7; but see Parker et al. 1983). Thus, as in the north after hare populations have crashed, lynx in southern boreal regions probably occupy relatively large home ranges in response to low-density hare populations.

Exploratory Movements

Occasionally, lynx in southern populations make what appear to be "exploratory" movements in which they make long-distance movements beyond their normal home range boundaries and subsequently return to their home range. Among eight lynx (six males, two females) studied in Montana, one juvenile and three adult males made exploratory movements ranging from 17 to 38 km in straight-line distance (Chapter 11). The duration of exploratory movements varied from one week to several months. All adult movements were initiated in July, but the juvenile made two exploratory movements; one between 18 March and 2 April and a second from about 21 July to 20 August. In the Wyoming study, an adult male left his home range in mid-June and returned in early September and an adult female left hers in early July and returned by early August; the geographic extent of these movements is unknown, however (Chapter 11). In the southern Canadian Rockies, a juvenile female made an exploratory movement of 38 km in straight-line distance in the fall prior to dispersing (C. Apps, personal communication).

Exploratory movements of this kind have not been reported from the taiga (Chapter 9). We speculate that in montane boreal forests, the distribution of high-quality lynx habitat is patchy and fragmented due to high amounts of topographic relief and variation in habitat conditions resulting from natural disturbance processes (Chapter 3). Under such conditions, dispersal in different directions would be expected to have varying probabilities of success. Thus, in montane systems with high amounts of spatial heterogeneity, dispersal success may be enhanced by exploratory movements to locate suitable habitat.

Dispersal

Dispersal is the movement of a organism (either juvenile or adult) from a place of residence to its first or subsequent breeding site (Shields 1987). Data on lynx dispersal in southern boreal forests are scanty and anecdotal in nature, and no successful dispersals (i.e., where a lynx has bred after moving to a new location) have been reported from southern boreal forests. Consequently, presumed dispersals may simply represent long-distance movements that were cut short when the animal died. Between late April and November, a female lynx dispersed a distance of 325 km from Montana to British Columbia, where it was trapped (Brainerd 1985, unpublished). A male lynx dispersed 97 km in Montana before it was trapped (Smith 1984, unpublished). In north-central Washington, an adult male and female lynx that were both resident in the study area for at least a year dispersed north

into British Columbia, where they were trapped 616 and 80 km north of the study area, respectively (Brittell et al. 1989, unpublished; J. Brittell, personal communication). Apps (Chapter 12) described three dispersal movements in the southern Canadian Rockies, including a juvenile male that dispersed 44 km in March and then remained in the new location for 31 days before his death; a juvenile female that moved 17 km over three days in March and occupied the new area for 15 days before her death; and a juvenile female that dispersed 55 km before contact was lost. Mech (1977) reported a 483-km movement by a female lynx that was radio-marked in northeastern Minnesota in 1974 and trapped in western Ontario in 1977.

Dispersal distances reported from southern boreal forests are comparable to those in the taiga, where movements >100 km are considered typical (Chapter 9). Apps (Chapter 12) suggested that steep terrain and the Trans-Canada Highway may affect dispersal movements. However, four of five lynx that dispersed in Montana, Washington, and Minnesota (Brainerd 1985, unpublished; Brittell et al. 1989, unpublished; Mech 1980; Smith 1984, unpublished) crossed either two- or four-lane highways and major rivers before they were trapped. Mowat et al. (Chapter 9) also reported that dispersing lynx in northern forests often crossed roads and large rivers and lakes, even during the snow-free season.

Demographic Characteristics

The most reliable information available on demographic characteristics for southern lynx populations comes from the successive field studies conducted by Brittell et al. (1989, unpublished) and Koehler (1990) in north-central Washington in the 1980s. Brittell et al. (1989, unpublished) monitored a total of 23 lynx with radiotelemetry in north-central Washington from 1980 to 1983. Among 12 resident females, none were known to have given birth to kittens during the course of the study. However, snow tracking indicated that an unmarked female was accompanied by two kittens in the winter of 1980-1981 and again in 1982-1983; no tracks of kittens were found in 1981-1982. Snow tracking was not conducted in the winter of 1983-1984 but, in August 1984 after field work was terminated, kittens were observed on two separate occasions: one radio-marked and one unmarked female were each accompanied by two kittens in or near the study area. Thus, from 1980 to 1984 at least eight kittens (mean litter size = two) were produced in a population estimated to contain 23 resident lynx each year of the three-year study. The study area was 1,161 km^2 in extent, resulting in an estimated density of 2.0 lynx / 100 km^2. Among radio-marked lynx, 12% were identified as transients; thus, total lynx density, including kittens and transients, was

estimated at 2.4 lynx / 100 km^2. During the course of this study, three females and one male died from natural causes; the mean annual mortality rate for radio-marked lynx was estimated at 11% (range = 0-29%).

Koehler (1990) continued radiotelemetry work on Brittell et al.'s study area from 1985 to 1987, monitoring a total of seven lynx (five males, two females). During both years of the study, 15 adults were known to occupy the central portion of the study area (648 km^2), at an estimated density of 2.3 adults / 100 km^2. No kittens were observed in the study area during winter 1985-1986, but in 1986-1987, snow tracking indicated that four kittens were present in the study area, resulting in an estimated mean annual density for adults and kittens of 2.6 lynx / 100 km^2. In 1986, both radio-marked females had litters of three and four kittens each. Both females gave birth again in 1987, one to a single kitten and the other to at least one kitten (actual litter size could not be determined); thus, mean litter size over both years of the study was at least 2.7 kittens. In addition, an uncollared female was accompanied by three kittens in the winter of 1986-1987. From snow tracking in the winters of 1986-1987 and 1987-1988, Koehler determined that only one of eight kittens from the three litters of known size survived to the following winter, resulting in an estimated kitten mortality rate of 88%. Two radio-marked adult males died during the course of the study, one from predation and another from unknown causes. Annual mortality rates for radio-marked adult lynx were 27% in 1986 and 0% in 1987. Thus, the estimated mortality rate for kittens was six to seven times higher than the mean mortality rate for radio-marked adults.

Both reproductive rates and kitten survival rates appear to be similarly low in other regions of the southern boreal forest where lynx have been studied. None of three adult female lynx captured by Apps (Chapter 12) in the southern Canadian Rockies in November of 1997 or 1998 were travelling with kittens; however, one radio-marked female was observed with a kitten in August 1998. Four unmarked family groups were detected in the study area (>3,000 km^2) in 1997, each of which contained two kittens. Both kittens (one male, one female) from one of the family groups were subsequently radio-marked, but neither survived to the spring of 1998. All resident adults survived through both years of the study, but a dispersing female kitten and a transient juvenile male died of starvation in the spring of 1998; a male kitten was killed by a predator in December 1997. None of the three adult female lynx monitored with radiotelemetry by Brainerd (1985, unpublished) in Montana from 1982 to 1984 gave birth to kittens. Only one out of four female lynx monitored during 1998 in Montana was known to have given birth (Chapter 11); after radio contact with this female was lost during the breeding season, she was relocated in late September 1998 with two kittens. The adult female radio-marked in Wyoming (Chapter 11) gave birth to a

litter of four kittens (two males, two females) on about 27 May; all four were still alive on 14 June when they were ear-tagged, but none survived into the winter.

Other information on productivity in lynx populations in southern boreal forests comes from carcass studies. Brainerd (1985, unpublished) examined placental scars and corpora lutea in 18 female lynx carcasses from Montana ranging in age from 1.5 to 9.5 years. Based on placental scars, the average litter size increased with age: yearlings had a mean litter size of 1.75 (range = 1-3), whereas mean litter size for adults was 3.25 (range = 1-5). Ovulation rates were also higher for adults, increasing from 3.22 (range = 2-5) for yearlings, to 5.33 (range = 2-9) for adults. The pregnancy rate for adults was 100%, whereas only 44.4% of uteri from yearlings contained placental scars.

Parker et al. (1983) examined 154 lynx carcasses obtained from trappers in Nova Scotia over three winters: 1977-1978 ($n = 42$), 1978-1979 ($n = 57$), and 1979-1980 ($n = 55$). The oldest lynx were 11 years old, but <6% of the sample was older than six years in any year. Over the three years of the study, the percentage of kittens in the sample declined from 29% to 9%, and 2%. Based on counts of placental scars, mean litter size was 3.2 for yearlings and 3.6 for adults; neither differed significantly among years. Overall pregnancy rates were 68% for adults and 27% for yearlings. However, yearling pregnancy rates declined from 67% in 1977-1978 to 29% in 1978-1979 and 0% in 1979-1980, whereas adult pregnancy rates only declined from 75% to 64%. Declines in the overall breeding and recruitment rates, as well as the reproductive success of yearlings, was attributed to a dramatic decrease (about six-fold in the best habitats) in the abundance of snowshoe hares over the course of the study (Parker et al. 1983).

With few exceptions, demographic parameters reported from southern boreal forests are comparable to those occurring in the taiga during times of hare scarcity. The low in-utero litter sizes (3.25-3.6), low yearling pregnancy rates (27-44.4%), low yearling litter sizes (1.75-3.2), low kitten production, high kitten mortality rate (88%), and low lynx densities (Table 13.3) reported from southern populations are all characteristic of northern populations during hare lows. In the North, peak lynx densities vary from eight to 45 lynx/100 km^2 depending on habitat conditions, but drop to <3 lynx/100 km^2 during hare population lows, regardless of habitat quality (Chapter 9). Density estimates for lynx in north-central Washington ranged from 2.0 to 2.6 lynx/100 km^2 and remained relatively constant over the course of the seven-year study (Brittell et al. 1989, unpublished; Koehler 1990). The apparent stability of this low-density population has led to speculation that, because hare populations also occur at low levels in most southern boreal forests, lynx populations in the western mountains may not exhibit the cyclic fluctuations characterisitic of northern populations (Koehler and

Table 13.3—Densities of Canada lynx populations in North America.

Study area	Lynx density (lynx/100 km^2)	Source
Southern boreal forests		
North-central Washington	2	Brittell et al. 1989, unpublished
North-central Washington	3	Koehler 1990
Cape Breton Island, Nova Scotia	20[a]	Parker et al. 1983
Northern boreal forests during low snowshoe hare densities		
Central Alberta	2	Nellis et al. 1972, Brand et al. 1976
South-central Northwest Territories	3	Poole 1994
South-central Yukon	3	Slough and Mowat 1996
Southwestern Yukon	2	O'Donoghue et al. 1997
Kenai Peninsula, Alaska	4[b]	Kesterson 1988, unpublished
Interior Alaska	2-6	Stephenson 1986, unpublished
Northern boreal forests during high snowshoe hare densities		
Central Alberta	10	Nellis et al. 1972, Brand et al. 1976
South-central Northwest Territories	30	Poole 1994
South-central Yukon	45	Slough and Mowat 1996
Southwestern Yukon	17	O'Donoghue et al. 1997
Kenai Peninsula, Alaska	18	Kesterson 1988, unpublished

[a]Snowshoe hare densities were comparable to those occurring during population highs in northern boreal forests.
[b]Calculated from author's description of lynx abundance.

Aubry 1994). However, we caution that data bearing on this hypothesis are extremely limited; furthermore, a recent review of snowshoe hare density data in southern boreal regions (Chapter 7) and lynx trapping records from Washington, Montana, and New Hampshire (Chapter 8) suggest that both snowshoe hare and lynx populations may fluctuate more in number in the south than believed previously. Whether observed patterns reflect changes in resident lynx populations or immigrations from other areas, however, is unknown (Chapter 8). Understanding the nature of lynx population dynamics in southern boreal forests is a critical research need.

Human Impacts

Trapping

Little is known about the effects of trapping or shooting mortality on lynx populations in southern boreal forests. However, in recent years, concern over the conservation status of lynx throughout the contiguous United

States has resulted in severe restrictions on legal harvest; all states except Montana have either given lynx complete protection or closed their trapping season. In Montana, a statewide quota of 135 lynx was imposed in 1982; this quota was lowered steadily until 1991, when it was reduced to two lynx per year. Although legal harvest is no longer a conservation concern, human-caused mortality is believed to be additive in the low-density lynx populations characteristic of southern boreal forests (Koehler 1990; Table 13.3). If so, illegal or incidental harvest could significantly reduce population numbers of lynx in southern regions.

Roads and Trails

Roads into areas occupied by lynx may pose a threat to lynx from incidental harvest or poaching (Koehler and Brittell 1990), increased access during winter for competing carnivores, especially coyotes (Chapter 4), disturbance or mortality from vehicles, and loss of habitat. Although we know little about the indirect effects of roads or trails on lynx, none of the 89 lynx studied with radiotelemetry in Washington (Brittell et al. 1989, unpublished; Koehler 1990), Montana (Brainerd 1985, unpublished; Koehler et al. 1979; Smith 1984, unpublished; Chapter 11), Wyoming (Chapter 11), the southern Canadian Rockies (Chapter 12), Minnesota (Mech 1980), or Nova Scotia (Parker et al. 1983) were killed in vehicle collisions. Among 37 radio-marked animals that died during these studies, 19 were shot or trapped, eight died of starvation, six from predation, and four from unknown natural causes. Vehicle collisions were a significant mortality factor among 83 lynx translocated into the Adirondack Mountains of New York from the Yukon between 1989 and 1991; in the two years that translocated lynx were monitored with radiotelemetry, 16 were road-killed (K. Gustafson, personal communication). However, because translocated lynx may be especially vulnerable to vehicle collisions (Brocke et al. 1991), the high incidence of road-kills among lynx in this reintroduction effort is probably not representative of resident lynx populations in southern boreal forests.

In Nova Scotia, Parker (1981) found from snow tracking that road edges and forest trails were often followed by lynx for considerable distances, and similar observations were made during winter in Washington for roads less than 15 m wide (Koehler and Brittell 1990). From analysis of sequential telemetry locations for lynx in Washington, McKelvey et al. (Chapter 10) concluded that selection or avoidance of roads could not be inferred. Roads in the study area were of primitive standards that received little use in summer but were frequently used by snowmobilers in winter. Ongoing research by Apps (Chapter 12) in the southern Canadian Rockies suggests, however, that paved roads may have an influence on lynx spatial organization.

The 70% adaptive kernel home-range contour for two males and two females coincided with the Trans-Canada Highway; for another male, it coincided with a secondary highway.

Mowat et al. (Chapter 9) reported similar observations concerning roads in northern boreal forests; lynx appeared to tolerate moderate levels of snowmobile traffic, readily crossed highways, and established home ranges in proximity to roads. Several studies of lynx in the taiga have been conducted in areas of relatively dense rural human populations and agricultural development, suggesting that lynx can tolerate moderate levels of human disturbance.

Predation and Competition

Only a few instances of predation on lynx have been reported from southern boreal forests, but all are believed to have been by felids. Two of six mortalities reported from ongoing radiotelemetry studies in Montana were predation by mountain lions; both occurred during the snow-free period, including an adult male killed in May and a juvenile male killed in October (Chapter 11). An adult female lynx found dead in Montana in late January during an earlier study was believed to have been killed by a mountain lion (Koehler et al. 1979). A juvenile female lynx found dead in November in north-central Washington was believed to have died from a bite on the top of her skull by either a bobcat or a lynx (Brittell et al. 1989, unpublished), and an adult male was apparently killed by an unknown predator in January (Koehler 1990). In the southern Canadian Rockies, a male kitten was apparently killed by an unmarked male lynx in December (Chapter 12).

Cannibalism has also been reported from the taiga and generally occurs during periods of low hare abundance. In the north, wolverine, wolves, and coyotes have also been reported to prey on lynx (Chapter 9). Because mountain lions do not occur in most portions of the northern boreal forest or eastern United States (Dixon 1984), the potential effects of predation or competition from mountain lions are unique to lynx populations in the western mountains. Mountain lions are known to occupy high-elevation lynx habitats during both summer and winter. In a comparative study of habitat use by mountain lions, bobcats, and coyotes in central Idaho, Koehler and Hornocker (1991) found that a larger proportion of mountain lion locations (28%) were in high-elevation subalpine fir-whitebark pine habitats during summer than either bobcat (10%) or coyote (3%) locations. They also noted that, because of their body size, mountain lions could negotiate deeper snows than could other predators, enabling the mountain lions to better exploit higher elevations and mesic habitats where deep snows accumulated.

Mountain lions are present in lynx summer home ranges in Montana (Chapter 11), but interactions between them have not been studied.

Lynx and bobcats are generally believed to be spatially separated by snow depth, but several cases of these two species occupying the same area and presumably competing with one another for food and space have been documented in the western mountains (Smith 1984, unpublished; Brittell et al. 1989, unpublished). Parker et al. (1983) reported that the contraction of lynx range on Cape Breton Island in Nova Scotia was coincident with colonization of the lowlands by bobcats; in 1983, lynx only occurred in the highest elevation areas where bobcats had not established themselves. However, this appears to represent the authors' speculations only; no data to support this statement are presented. Although coyotes are potentially significant competitors of lynx (Chapter 4), evidence indicating that coyotes have negatively affected lynx populations in southern boreal forests is lacking.

Competition between lynx and other mammalian or avian predators does not appear to strongly influence lynx populations in the taiga (Chapter 9), probably because of the cyclic nature of snowshoe hare populations (which mediates the effects of exploitation competition), and the relative scarcity of many of the mammalian predators likely to compete strongly with lynx (Chapter 4). Buskirk et al. (Chapter 4) have discussed the potential for detrimental effects on lynx populations from increased competition with generalist predators in landscapes disturbed and/or fragmented by human activities. If such competition can have a significant effect on lynx populations, we speculate that it may be of particular concern in western montane regions of the southern boreal forest. In that area, lynx are sympatric with the three potentially strongest competitors: mountain lions (interference competition), bobcats, and coyotes (exploitation competition), all of which are generally increasing in number (Chapter 4). However, this concern is largely conjectural; data on the effects of sympatric carnivores on lynx populations in southern boreal forests are rare.

Conclusions

In this chapter, we considered all lynx studies conducted south of the Polar Ecoregions in North America (Bailey 1998), including those in Nova Scotia, Minnesota, and the western montane regions. However, results from Nova Scotia differed strongly in many ways from studies conducted in other southern boreal forests (see Tables 13.1, 13.2, 13.3), and were most similar to studies conducted in the taiga during snowshoe hare population peaks. Results from western montane regions, where snowshoe hare populations

generally occurred at relatively low densities, were similar among studies, and generally comparable to those reported from the taiga during hare population lows. For these reasons, results from lynx studies in Nova Scotia are probably more representative of taiga populations than those in the western montane regions.

In general, southern lynx populations appear to be distinguished from those in the taiga primarily by differences in the quality and distribution of available habitat: their primary prey, the snowshoe hare, typically occurs at very low densities and, because of differences in topography and natural disturbance regimes, habitats containing abundant snowshoe hare populations are more patchily distributed than in the taiga. As a result, their food habits, home range sizes, densities, and reproductive characteristics are generally comparable to those reported for northern lynx populations during times of hare scarcity. Differences in lynx ecology between populations in the taiga and those occurring in southern boreal forests appear to be related primarily to the use of alternative prey species, the effect of habitat patchiness on movements, reproduction and survival, and the potential effects of different communities of predators and competitors on lynx populations.

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