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    THE SHARP-SHINNED HAWK (ACCIPITER ATRIATUS VIEILLOT)
    IN INTERIOR ALASKA

UNIVERSITY OF ALASKA   M.S. 1984

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THE SHARP-SHINNED HAWK

(Accipiter striatus Vieillot)

IN INTERIOR ALASKA

A

THESIS

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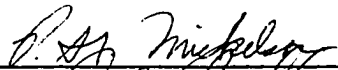
for the Degree of

MASTER OF SCIENCE

By

Ronald Gordon Clarke, B.S.

Fairbanks, Alaska

May 1984

THE SHARP-SHINNED HAWK

(Accipiter striatus Vieillot)

IN INTERIOR ALASKA

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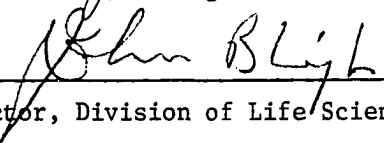
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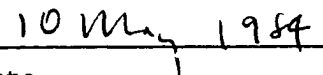Program Head, Biological Sciences

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ABSTRACT

Breeding ecology of sharp-shinned hawks (Accipiter striatus) was studied at nineteen nests in interior Alaska from 1978 to 1981. Hawks nested in conifers in dense, young stands of mixed deciduous and coniferous trees. Sharp-shins primarily ate small birds, apparently hunted the most productive habitats and captured prey in proportion to availability. Growth and food requirements of four captive-reared nestlings were monitored to supplement data on wild young. A typical family required an estimated 13,620 g of prey during the breeding season. In comparison to other studies, Alaskan sharp-shinned hawks 1) reoccupied old nest areas more frequently, 2) occupied smaller home ranges, 3) nested in greater densities, 4) completed breeding cycles more quickly, 5) laid more eggs and 6) hatched and fledged more young. In future studies, which are important because of the sharp-shin's extensive range and susceptibility to pollution and habitat destruction, Alaskan birds could serve as standards of comparison.

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PREFACE

Bent (1937) described the sharp-shinned hawk (<u>Accipiter striatus</u>) as an "impudent villain", "...the terror of all small birds and the audacious murderer of young chickens...", a bird fond of "...beating stealthily about the shrubbery to the fatal surprise of many a little songster". Unfortunately, this dim view of sharp-shins was long held by many naturalists, and, all too often, when an individual was seen, "...the hawk's career was promptly ended by a charge of shot" (R. B. Simpson 1911 <u>in</u> Bent 1937). Major Allan Brooks (1919) exemplified this primitive attitude:

> May I make a small correction in Mr. Law's recent account of the incident he relates on p. 27 of THE CONDOR for January-February, 1919? The hawks were Sharp-shinned not Cooper, the third female was a bird of the preceding year in the first plumage, and it, together with the male, was also shot, making a clean sweep of these pestiferous destroyers.
>
> At the risk of being quoted as an awful example by the ultra-protectionists of the "balance of nature" school, I must repudiate any desire, whether prompted by curiosity or otherwise, of seeing an Accipiter raise a brood--I know too well at what a sacrifice of small bird life this result would be achieved.

Brooks wrote these words 37 years to the day before I appeared on the face of this planet. Luckily, in that time, scientific thought and ecological perspectives had advanced a great deal. I offer this paper as a celebration of the happy and eternal demise of the narrow and muddled sort of thinking displayed by Major Brooks.

For this paper, I have chosen not to capitalize bird names. Even in the face of years of tradition, staunchly upheld by major ornithological journals, I fully concur with Atkin's (1983) assertion

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that, in regard to capitalization of bird names, it is "...a source of embarrassment for birders to have to follow rules that contradict the usage in the world at large...". I hope readers will not be Unduly Offended.

One cannot conduct a long-term study of accipiters without enlisting the help of others. Many friends and colleagues, both at the University of Alaska, Fairbanks and elsewhere, contributed to this study. I would like to thank them all, especially the following:

My major advisor, Dr. L. Gerard Swartz, whose role as field companion, tree climber, bird babysitter, purveyor of inspiration, editor and friend has been greatly appreciated.

Graduate advisory committee members Dr. R. Dale Guthrie and Dr. Peter G. Mickelson, for their guidance and suggestions.

My parents, Mardelle A. and Gordon F. Clarke, who provided continual moral support, patience and encouragement, as well as an occasional stake for a few dollars when things were lean.

Larry L. Hanson and Dr. Patrick T. Redig, who encouraged my interest in science, the outdoors and birds of prey when I was just beginning to appreciate the fascination and complexity of the natural world.

Beverly R. DeVore and Anne C. Seguin, who were invaluable field assistants, especially during early-morning trips to observation blinds.

The impeccably organized Peter J. Bente, who helped with field

logistics and very literally made possible the radio-tracking portion of this study.

Alan M. and Martha I. Springer, David G. Roseneau, Dr. Edward C. Murphy and Dr. Douglas N. Weir, all of whom provided helpful suggestions and field assistance.

Daniel D. Gibson, Stephen O. MacDonald and Dr. Brina Kessel, who assisted me in identifying sharp-shinned hawk prey remains.

Scott M. Brainerd, Laurence C. Byrne, Celeste Sozoff, Donald J. Vernam and Cortland R. Zachel, who helped with the radio-tracking of hawks in 1979.

Herbert and Hilda Melchior, Hal J. Trost and Cortland R. Zachel, who provided me with nest locations that would otherwise have gone unnoticed.

An unknown UAF student, who fell on and broke my knee during an intramural football game. This prevented me from studying merlins (Falco columbarius) as originally planned, and allowed me to remain in the Fairbanks area, where I discovered the fascinating world of small accipiters.

Betty A. Anderson and Lesley J. DeKrey, who typed the various drafts of this thesis and offered valuable editorial advice.

I extend special thanks to Gail J. and William R. Tilton, whose friendship and assistance throughout this study has been a steady source of encouragement, reassurance, confidence and great pleasure. Gail's talent for maintaining a positive attitude despite screaming

hawks, frantic dogs and tired field biologists kept us all from losing
our minds in the name of science, and Bill's field expertise, keen eye,
unquenchable enthusiasm and uncanny ability to think like an accipiter
contributed immeasurably to the overall success of this study. I am
pleased to dedicate this thesis to them.

INTRODUCTION

Sharp-shinned hawks are the smallest of the North American ac-
cipiters, a genus characterized by birds with short wings and long
tails--forest dwellers which prey on birds and mammals. Sharp-shinned
hawks breed in coniferous forests and mixed woodlands from the tropics
to the subarctic treeline (Brown and Amadon 1968), and may be the most
abundant raptors in North America (Beebe 1974).

Sharp-shinned hawks are highly migratory and eat mostly migrant
prey. In other raptors, this results in accumulation of pollutant
residues in body tissues, with potentially detrimental effects (Cade
et al. 1971, Snyder et al. 1973, Newton 1979, Swartz et al. 1977,
Newton et al. 1979). Even though no widespread, long-term effects of
pesticide pollution on population levels of sharp-shins have been
documented (Peterson 1969), declines in numbers have been noted at
counting and banding stations (D. L. Evans, pers. comm.), and the
species has been "blue-listed" by the National Audubon Society since
1971 (Anonymous 1971, Tate and Tate 1982).

Because of its extensive range and apparent sensitivity to
environmental pollution and habitat destruction, the sharp-shinned hawk
is in a position to serve well as an indicator of continent-wide
environmental quality trends. However, the huge potential data base
provided by sharp-shinned hawks has gone virtually unnoticed. To
facilitate compilation and understanding of this data base, it is
important that certain base-line parameters be defined, so future

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changes may be recognized.

Rust (1914), Storer (1955), Craighead and Craighead (1956), Storer (1966), Mueller and Berger (1967, 1970), Reynolds (1972), Platt (1973), Snyder and Wiley (1976), Platt (1976), Reynolds (1978), Reynolds and Wight (1978), Mueller et al. (1979, 1981) and Reynolds et al. (1982) have reported on various aspects of sharp-shinned hawk biology, but there has been no attempt to integrate a comprehensive picture of its ecology. It is my purpose, in this paper, to define the breeding ecology of the sharp-shinned hawk in interior Alaska. Since Alaska is less developed and less disturbed than most areas on the continent, it may provide the closest available approximation to "optimal" breeding conditions. Thus, sharp-shinned hawks in this study may serve as a standard against which sharp-shinned hawks elsewhere could be compared.

STUDY AREA

Most field work was done within 8 km of the campus of the University of Alaska, Fairbanks ($64^{\circ}52'$ N., $147^{\circ}49'$ W.), and on a 12 ha hillside 110 km southeast of Fairbanks on the Richardson Highway ($64^{\circ}18'$ N., $146^{\circ}22'$ W.). Both areas are at the edge of the Yukon-Tanana uplands, and consist of rolling hills rising from the floodplain of the Tanana River. Data were collected opportunistically from other areas.

The taiga of interior Alaska is a highly heterogeneous mosaic of small patches of various vegetation types (Neiland and Viereck 1977, Foote 1983). This mosaic results from the interaction of permafrost conditions, directional exposure of hillsides, soil water content, depth of organic matter, river meanderings, flooding, fire history, human disturbance and climate. These factors combine to create specific microclimates, which manifest themselves as different vegetation types.

This diversity of vegetation results in a wide variety of avian habitats. According to Kessel's (1979) classification scheme, twelve major avian habitat types occur in the study area: "wet meadow", "dwarf shrub meadow", "grass meadow", "dwarf shrub mat", "low shrub thicket", "medium shrub thicket", "tall shrub thicket", "deciduous forest", "coniferous forest", "mixed decidous coniferous forest", "scattered woodland and dwarf forest" and "artifical habitats". Variations in species composition within these major types create many different "subtypes", providing habitat both for sharp-shinned hawks and for the

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prey animals they eat.

METHODS

Field work began on 25 June in 1978, 25 April in 1979, 1 May in
1980, and 20 May in 1981, and continued until 23 September in 1978, 26
September in 1979, 4 September in 1980 and 1 September in 1981.
Historic nesting areas were searched each season for signs of occupancy
such as molted feathers, droppings, remains of prey, regurgitated
castings, recently-built nests and the birds themselves. Reports of
sharp-shinned hawk sightings were solicited from other biologists,
birdwatchers and outdoor enthusiasts; each report was followed by a
search for nesting hawks. I also explored areas with vegetation and
topography similar to known nesting areas.

In this study, nest site is defined as "the area surrounding the
nest tree, including the vegetation and topographic features, used by
a nesting pair during an entire nesting season, exclusive of foraging
areas" (Reynolds et al. 1982). Nest sites were named for nearby
physiographic or human-built features and qualified with the year of
activity (Table 1). An area containing several different nest sites
situated within 100 m of the nearest neighboring site is referred to
as a "nest area".

Bird names are according to the American Ornithologists' Union
(1983). Terms for developmental stages of birds follow Skutch (1961).
Plant names follow Hultén (1968). All times noted are Alaska Daylight
Time (ADT). The reader should be aware that, in 1983, all areas in-
volved changed to Yukon Time.

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Table 1. Key to sharp-shinned hawk nest sites, interior Alaska, 1978-
1981.

Name	Identifying Feature
Backyard	L.G. Swartz residence
Banner Creek	Banner Creek
Chena	Chena Small Tracts Road
Dogpatch	Ballaine Hill residental area
Campus	Geophysical Institute, University of Alaska, Fairbanks
Melchior	H.R. Melchior residence
Moose Creek	Moose Creek Bluff
Salcha	Salcha River
Springer	A.M. Springer residence
Trost	H. Trost residence

I. BREEDING BIOLOGY

Nesting activities and behavior were observed at one nest site in each of the first three seasons. In 1978, a blind was built on the ground 20 meters (m) from a nest tree. A similar blind was placed 10 m from a nest tree in 1979. In 1980, a tree blind was built 5 m from and level with an active nest. The first two seasons, an assistant accompanied me to the blind; we entered the blind, then the assistant left, attempting to create the illusion that the blind was empty. Birds often screamed and sometimes dived at us upon arrival and at the departure of the assistant, but behaved "normally" when I was alone in the blind. In 1980, I traveled alone to and from the blind. The birds usually attacked me as I climbed, but ignored me once I was inside. During the post-fledging period, both young and adults occasionally perched on the roof of the blind, implying that it and its occupant were not sources of lasting disturbance.

Whenever possible, free flying hawks were captured, weighed, measured, banded, photographed and released. One fledgling was hand-caught after she stunned herself flying into a woven-wire fence near the Campus 1978 observation blind. Molt patterns of breeding birds were noted whenever they could be observed closely.

Nesting activities were observed from blinds on 37 separate days for a total of 172.2 hours (h). In 1979, 97.9 h of observation were accumulated during 16 days of the nestling period and 43.3 h during 15 days of the fledgling period. In 1979, observation was limited to 8.3

h during 3 days of the incubation phase. In 1980, a nest was observed for 20.2 h during 3 days of the nestling period and 2.5 h during 2 days of the fledgling period.

Nest sites were visited at least twice weekly until young dispersed, except that the Banner Creek nests were visited only every three to four weeks.

Each nest site was plotted on a 1:63,360 scale topographic map to estimate latitude and longitude to the nearest minute, and elevation to the nearest 10 m.

The habitat surrounding each nest was quantitatively assessed according to methods described by James and Shugart (1970), except that center points of 0.04 ha plots were not chosen randomly, but were defined by the nest tree(s).

Nest trees were measured for diameter at breast height (DBH), height, and height of nest platform. Age of nest trees at ten randomly-selected sites was estimated using an increment borer. Five to twenty other trees at each of those ten sites were also cored to determine age. Nest width, maximum thickness and depth of nest cup were measured. Axial width was measured from the trunk of the nest tree from inner to the outer nest edge. Radial width was measured perpendicularly to axial width. For width measurements, nests built between trunks of two or more closely-situated trees were treated as if the largest tree were the only one present. Directional exposure, i.e., on which side of the tree the nest was placed, and construction

materials were noted.

Characteristics and locations of plucking perches were noted, as were any other distinguishing features of each nest site.

Using radio telemetry, I followed the Backyard 1979 pair during the late nestling period, when I assumed the adults would be hunting extensively and the home range would be at its maximum. The male was tracked for four days, the female for seven. Home range size was estimated by calculating the area of a circle having the nest tree as its center and the most distant radiolocation at its edge.

Nesting density was estimated by calculating the mean distance between nearest neighbor nests in 1979 and 1980 (four nests each year). This value was assumed to be the diameter of a typical circular home range. I calculated the area of that circle and divided it into 100 km^2 to estimate the number of breeding pairs per 100 km^2.

During egg-laying, I inspected three nests daily, either with a small parabolic mirror affixed to a 10 m pole or by climbing. Inspections were cancelled and females were not flushed from eggs in inclement weather. I climbed to eight nests at least once during incubation and to eleven nests during the nestling period to count eggs and/or young.

When possible, eggs were measured and weighed. Some eggs were weighed two or three times over the incubation period to determine weight loss from laying to hatching.

To assess any differences in size or thickness of Alaskan sharp-

shinned hawk eggshells as compared to other, older, shells, I traveled to the Western Foundation of Vertebrate Zoology in Los Angeles, California and measured 69 sets of eggs (n=302) collected from across North America trom 187ɔ to 1960. In addition to external dimensions and weight, shell thicknesses of 301 eggs were measured directly using a modified bench caliper. Readings were also taken at three points on these eggs with a beta-backscatter counting device. For eggs I found in the field, backscatter counts were taken on two addled eggs in 1979 only, as the device was only briefly available. I collected three large rragments of hatched eggs, one in 1978 and two in 1979, and later measured these with both the beta-backscatter device and the bench calipers.

Synchrony of hatching was determined either by observing the eggs and young the day(s) of hatching, or by comparing the weights and measurements of skeletal elements of older nestlings. Ages of young were calculated as if the first portion of a day out of the egg was "day 0" and the first full 24 h out of the egg was "day 1". Young at 9 nests (5 in 1979 and 4 in 1980) were measured at intervals of two to six days. When hawks were old enough to perch on nearby branches, climbing ceased to avoid causing premature fledging.

In 1979, growth of four hand-reared sharp-shinned hawks was closely monitored. Food intake and weight gain were recorded at every feeding, and daily measurements of skeletal elements and feathers (Baldwin et al. 1931, Olendorff 1972) were taken on each bird. Fresh-

killed songbirds were fed to the hawks; when these were unavailable, Japanese quail (<u>Coturnix japonica</u>) were substituted.

Weights of full crops of captive young were calculated after each feeding by subtracting pre-meal weight from post-meal weight of each bird. These were used to estimate weight of food in wild nestlings' crops, which was subtracted from total weight to give true weight of wild nestlings.

Measuring of captive young ceased at 23 days of age, when they began serious attempts at flight. They were placed in an artificial nest outdoors and allowed to develop and, ultimately, disperse. Food was supplied liberally until birds had dispersed.

Nests were considered "successful" if at least one young reached the age at which it began moving out onto branches adjoining nests.

Dead sharp-shinned hawks were collected when available, and cause of death was noted at necropsy. Young missing from nests were assumed dead, and any evidence suggesting cause of death was noted.

II. FEEDING ECOLOGY

The diet of sharp-shinned hawks was assessed by analyzing remains of prey animals collected from nest sites. This technique has been employed by many researchers, and despite some shortcomings, it remains the most complete and accurate means of determining food habits (Errington 1930, 1932 and 1933, Munro 1940, Meng 1959, Sulkava 1964, van Beusekom 1972, Opdam 1975, Langvatn 1977, Opdam 1978, Reynolds 1978, Newton and Marquiss 1982a).

At each visit, I collected prey remains and regurgitated castings from plucking perches and the ground underneath nests. I collected remains from the nests themselves irregularly; after dispersal, all prey remains were collected from each nest. Materials from each perch, area, or nest were placed in separate plastic "whirl-paks" labeled with the date, time and location of collection. Contents were dried in an oven, identified using the University of Alaska Museum collection and evaluated so as to produce the most conservative number of individual prey animals represented. Castings were evaluated separately and not included with totals from other remains, because feathers or fur found at plucking perches could have been from the same prey items as bones found in castings, and some items might have been counted twice.

I separated avian remains into four age classes:

1. "Nestling" (young of the year, helpless): remiges/retrices fully sheathed

2. "Juvenile" (young of the year, capable of extended activity, but incapable of sustained flight): remiges/retrices at least one-third but not fully sheathed; immature coloration

3. "Immature" (young of the year, capable of sustained flight; full-grown yearlings in immature plumage): remiges/retrices less than one-third sheathed; immature coloration

4. "Adult" (full-grown adults): remiges/retrices fully developed; adult coloration

Mammalian prey were assigned to three age classes:

1. "<u>Juvenile</u>" (young of the year): long bones less than one-half adult length; subadult pelage

2. "<u>Subadult</u>" (full-grown young of the year and yearlings): long bones more than one-half but less than full adult length; subadult pelage

3. "<u>Adult</u>" (full-grown adults): complete bone development; adult pelage

Each prey item was assigned to a size class (Storer 1966):

 Class 1: 3.4 - 8.0 grams (g)

 Class 2: 8.0 -15.6 g

 Class 3: 15.6 - 27.0 g

 Class 4: 27.0 - 42.9 g

 Class 5: 42.9 - 64.0 g

 Class 6: 64.0 - 91.1 g

Weights for most adult avian prey species were from Spindler and Kessel (1978). Weights for the remaining avian and all mammalian prey species were from the University of Alaska Museum (UAM). Non-adult weights were estimated using weights of UAM specimens as a guide. I assumed that 1) weights of immature birds were comparable to those of adults, that juveniles weighed 50% of the adult weight and that nestlings weighed 25% of the adult weight; and 2) subadult mammals weighed 60% as much as adults and juveniles weighed 33% of the adult weight. For the remains of two juvenile snowshoe hares, weight was estimated by graphing known weights against known hind foot measure-

ments (UAM data) and then plotting the hind foot measurements from the
remains to locate approximate weight (Table 2).

Sources of local songbird abundance information (West and DeWolfe
1974, Spindler 1976, Spindler and Kessel 1980) were consulted to
estimate whether sharp-shinned hawks preyed upon local birds in the
proportions in which they occurred in a habitat. To determine if hawks
were concentrating foraging efforts spatially, every prey species was
assigned to a vegetation height zone on the basis of where each was
most likely to be encountered and to a foraging guild according to the
food habits of each. Zone and guild definitions used are according to
Reynolds (1978):

Foraging Zones	Foraging Guilds
1 - Ground/Lower Shrub	1 - Ground Searcher
2 - Upper Shrub/Lower Canopy	2 - Trunk Gleaner
3 - Upper Canopy	3 - Foliage Gleaner
4 - Aerial	4 - Hawker
5 - Generalist	5 - Aerial Insectivore
	6 - Generalist

Assignment to zones and guilds were made according to Reynolds (1978)
and Spindler and Kessel (1980). Habitat preferences of prey (Spindler
1976, Spindler and Kessel 1980) were noted to determine if sharp-
shinned hawks were concentrating hunting activities according to
habitat type.

To detect any seasonal changes in prey use, prey items were as-

Table 2. Weights, size class designations and zone/guild affiliations of species identified as sharp-shinned hawk prey in interior Alaska, 1978-1981.

Common and Scientific Names	Weight in Grams (Size Class[1])			Zone,[3] Guild
	Adult/Immature[2]	Juvenile	Nestling	
lesser yellowlegs, Tringa flavipes	80.5(6)	—	—	1, 1
solitary sandpiper, Tringa solitaria	51.5(5)	—	—	1, 1
spotted sandpiper, Actitis macularia	37.3(4)[4](n=6)	—	—	1, 1
downy woodpecker, Picoides pubescens	25.8(3)	—	—	3, 2
olive-sided flycatcher, Contopus borealis	34.1(4)	—	—	3, 4
western wood-pewee, Contopus sordidulus	13.5(2)[4](n=1)	—	—	3, 4
alder flycatcher, Empidonax alnorum	12.6(2)	6.3(1)	—	3, 4
Hammond's flycatcher, Empidonax hammondii	11.0(2)	5.5(1)	—	3, 4
tree swallow, Tachycineta bicolor	18.0(3)	—	—	4, 5
bank swallow, Riparia riparia	17.3(3)	—	—	4, 5
cliff swallow, Hirundo pyrrhonota	18.3(3)	—	—	4, 5
black-capped chickadee, Parus atricapillus	11.7(2)	5.9(1)	—	2, 3
boreal chickadee, Parus hudsonicus	11.5(2)	5.8(1)	—	2, 3
ruby-crowned kinglet, Regulus calendula	7.0(1)	—	—	3, 3
Swainson's or gray-cheeked thrush, Catharus ustulatus or C. minimus	28.8(4)	14.4(2)	—	1, 6
hermit thrush, Catharus guttatus	27.0(4)	—	—	1, 6
unidentified Catharus thrush, Catharus ustulatus, C. minimus or C. guttatus	28.2(4)	14.1(2)	—	1, 6
American robin, Turdus migratorius	88.0(6)	—	—	5, 6
varied thrush, Ixoreus naevius	78.5(6)	—	—	5, 6
Bohemian waxwing, Bombycilla garrulus	59.3(5)	29.7(4)	—	5, 6
orange-crowned warbler, Vermivora celata	9.5(2)	4.6(1)	—	2, 3
yellow warbler, Dendroica petechia	9.7(2)	4.9(1)	2.4(1)	2, 3
yellow-rumped warbler, Dendroica coronata	12.5(2)	6.3(1)	3.1(1)	3, 3
Townsend's warbler, Dendroica townsendi	9.4(2)	4.7(1)	—	3, 3

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Table 2. (continued)

Common and Scientific Names

blackpoll warbler, _Dendroica striata_
northern waterthrush, _Seiurus noveboracensis_
Wilson's warbler, _Wilsonia pusilla_
American tree sparrow, _Spizella arborea_
savannah sparrow, _Passerculus sandwichensis_
fox sparrow, _Passerella iliaca_
Lincoln's sparrow, _Melospiza lincolnii_
white-crowned sparrow, _Zonotrichia leucophrys_
dark-eyed junco, _Junco hyemalis_
Lapland longspur, _Calcarius lapponicus_
rusty blackbird, _Euphagus carolinus_
unidentified redpoll, _Carduelis flammea_ or _C._
  hornemanni
pine siskin, _Carduelis pinus_
unidentified, Class 1
unidentified, Class 1 or 2
unidentified, Class 2
unidentified, Class 2 or 3
unidentified, Class 3
unidentified, Class 4 or 5
unidentified, Class 1, 2, 3, or 4
unidentified shrew, _Sorex cinereus_, _S. monticolus_
  or _S. hoyi_

Weight in Grams (Size Class[1])			Zone, Guild[3]
Adult/Immature[2]	Juvenile	Nestling	
12.4(2)	6.2(1)	--	2, 3
17.3(3)	--	--	1, 1
7.7(1)	--	--	2, 3
17.9(3)	9.0(2)	--	1, 1
18.0(3)	9.0(2)	--	1, 1
36.6(4)	18.3(3)	9.2(2)	2, 1
15.8(3)	--	--	1, 1
24.0(3)	12.0(2)	--	1, 1
18.6(3)	9.3(2)	4.7(1)	5, 1
27.3(4)[4](n=23)	--	--	1, 1
48.9(5)	24.5(3)	--	5, 1
14.1(2)[4](n=65)[5]	7.1(1)	--	2, 6
12.2(2)	--	--	5, 3
7.4(1)	--	--	--
10.9(2)	5.5(1)	2.7(1)	--
12.1(2)	6.1(1)	--	--
15.0(2)	7.5(1)	3.8(1)	--
19.1(3)	9.6(2)	--	--
37.9(4)	--	--	--
18.0(3)	9.0(2)	4.5(1)	--
4.4(1)[4](n=106)[6]	2.6(1)	--	1, 1

$$\overline{X} = 3.5(1)$$

Table 2. (continued)

Common and Scientific Names	Weight in Grams (Size Class[1])			Zone,[3] Guild
	Adult[2]	Subadult	Juvenile	
northern red-backed vole, _Clethrionomys rutilus_	$26.5(3)^4$(n=63)	--	--	1, 1
meadow vole or tundra vole, _Microtus_ _pennsylvanicus_ or _M. oeconomus_	$31.0(4)_4^{}$(n=36)[7]	--	--	1, 1
meadow jumping mouse, _Zapus hudsonius_	$18.0(3)^4$(n=29)	--	--	1, 1
snowshoe hare, _Lepus americanus_	--	--	40.5(5)	1, 1
unidentified mammals (see text)	20.0(3)	12.0(2)	6.7(1)	

$$\overline{X} = 12.9(2)$$

[1]After Storer (1966):

   1 = 3.4- 8.0 grams (g)   4 = 27.0-42.9 g
   2 = 8.0-15.0 g   5 = 42.9-64.0 g
   3 = 15.6-27.0 g   6 = 64.0-91.9 g

[2]Weights from Spindler and Kessel (1978), non-adult weights estimated according to text.

[3]After Reynolds (1978):

    Foraging Zone   _Foraging Guild_
    1-Ground/Lower Shrub   1-Ground Searcher
    2-Upper Shrub/Lower Canopy   2-Trunk Gleaner
    3-Upper Canopy   3-Foliage Gleaner
    4-Aerial   4-Hawker
    5-Generalist   5-Aerial Insectivore
                         6-Generalist

[4]Weights from the University of Alaska Museum vertebrate collection, non-adult wts. estimated according to text

[5]_Carduelis flammea_ (n = 28), _C. hornemanni_ (n = 25), "redpoll" (n = 12)

[6]_Sorex cinereus_ (n = 86), _S. monticolus_ (n = 8), _S. hoyi_ (n = 12)

[7]_Microtus pennsylvanicus_ (n = 19) _M. oeconomus_ (n = 17)

signed whenever possible to half-month periods, beginning with May 1.

Remiges of _Catharus_ thrushes are distinctive and were easily
separated from other avian remains. _Catharus_-type remiges and rufous
retrices readily identified hermit thrushes (_Catharus guttatus_), but
Swainson's thrushes (_C. ustulatus_) and gray-cheeked thrushes (_C.
minimus_) were indistinguishable. Remains categorized as "Swainson's
or gray-cheeked thrush" were assigned a weight equal to the mean for
the two species. If no retrices were present, thrush remains were
termed "unidentified _Catharus_ thrush" and assigned a weight equal to
the mean for the three species. Remains of common redpolls (_Carduelis
flammea_) and hoary redpolls (_Carduelis hornemanni_) were in-
distinguishable, so all redpolls were placed into a "redpoll" category
and assigned a weight equal to the mean for the two species.

Shrew remains were placed into a "shrew" category and assigned an
adult weight equal to the mean for masked shrew (_Sorex cinereus_), dusky
shrew (_S. monticolus_) and pygmy shrew (_S. hoyi_). All shrew remains
were either adult or subadult, and the weight assigned was therefore
a mean of adult and subadult weight estimates. One item was either a
meadow vole (_Microtus pennsylvanicus_) or a tundra vole (_M. oeconomus_);
it was termed "meadow vole or tundra vole" and assigned a weight equal
to the adult mean for these two species.

Remains representing individuals that could not be identified to
species or to above-mentioned categories were termed "unidentified".
Avian remains were placed as specifically as possible into size and age

classes according to feather morphology. Mean weight for each size class was estimated by calculating the mean of the weights of prey species in each class. Unidentifiable mammalian remains could not be categorized by size class and were assigned an adult weight equal to the mean of the weights of the other mammalian prey, with the exception of the snowshoe hare, since no unidentified prey items were hares. Since age class was similarly indecipherable, they were assigned a weight equal to the mean of the three age class weight estimates.

I used Reynolds' (1978) energetics model (adapted from Wiens and Innis 1974) to estimate the amount of food required to sustain a typical sharp-shinned hawk family from the time adults arrive until young disperse:

Kendeigh's (1969) formula was used to estimate daily existence energy requirements for an adult hawk at $30^{\circ}C$:

$$M_{30} = 0.5404(W)^{0.7545} \text{kilocalories (kcal)}$$

where M is existence energy and W is body weight.

It was assumed that 70 percent of the energy intake was metabolically available (Kale 1965, Wiens and Innis 1974), so calculated existence energy was multiplied by 1.43. To account for the metabolic demands of activity, energetic cost was increased by 40 percent, so values were multiplied by 1.4 (Reynolds 1978).

To determine energetic cost of egg production (EC), egg weight (EW) was estimated according to Rahn et al. (1975):

$$EW = 0.741(W_{female})^{0.633}$$

Assuming egg production efficiency of 73 percent (King 1973, Wiens
and Innis 1974) and a caloric value of 1.05 kcal/gram (g) wet
weight (King 1973), total energetic demand for producing an
average clutch of eggs (CS) was

$$EC = EW \ (CS) \ (1.05) \ (1.37) \ kcal$$

Energetic cost of nestling growth (MN) was estimated at 20 per-
cent above existence energy (Wiens and Innis 1974), so for an
average brood (NS) over a typical nestling period (NP), energy
demand was

$$MN = M_{30} \ (1.20) \ (1.43) \ (NS) \ (NP)$$

Fledgling's existence energy (MF) needs increased less for
growth (5 percent) and more for activity (10 percent) (Reynolds
1978). Estimated energy demand for a typical number of fledglings
(FS) over an average fledgling period (FP) was

$$MF = M_{30} \ (1.15) \ (1.43) \ (FS) \ (FP)$$

Once dispersed, fledglings are essentially adults, so the ener-
getic requirement for the time between independence from the nest
site and departure on fall migration (MP) was estimated by sub-
stituting the length of the post-fledging period (PP) for the
length of the breeding season in the adult existence energy for-
mula:

$$MP = M_{30} \ (1.43) \ (FS) \ (PP)$$

Thus, the total energy requirement for a typical sharp-shinned
hawk family through an entire season was estimated as follows:

$$M_{male} + M_{female} \text{ (123 days)} + EC + MN + MF + MP$$

Required energy was converted to g of bird and mammal tissue assuming bird tissue = 1.757 kcal/g (Cummins and Wuycheck 1971) and mammal tissue = 1.501 kcal/g (Gorecki 1965).

RESULTS AND DISCUSSION

First-year sharp-shins are brown with buffy underparts streaked with brown. They begin molting into adult plumage at about ten months of age. Adults are bluish-gray above and white barred with orange below. Both adults and immatures have whitish spots on the shoulders and back. The eyes are yellow the first year, progressing to red with age. Their feet and toes are proportionally longer and narrower than those of their congeners, a trait presumably correlated with catching avian prey. However, they lack the power to be efficient killers, and often, prey succumbs as a consequence of being eaten.

Sharp-shinned hawks exhibit the strongest degree of reversed sexual size dimorphism seen in raptors, with females sometimes weighing almost twice as much as males (Table 3).

Nineteen active nests were located. Eleven were found by searching areas of past occurrence, six by searching where others had reported sighting adult birds and two by other investigators. Incidental, qualitative observations of 83 inactive nests showed characteristics similar to those described for active nests.

Interior Alaskan taiga is a highly heterogeneous mosaic composed of many patches of various vegetation types (Neiland and Viereck 1977, Viereck et al. 1982). Within that mosaic, sharp-shinned hawks typically nested in conifers in mixed stands of small to mid-sized deciduous trees, predominantly paper birch, which provided dense canopies over well-developed understories of smaller trees and shrubs.

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Table 3. Body weights of sharp-shinned hawks.

Location	Source	Sex	Weight (g)	n	SD
Alaska	This study	Male	103.2	2	5.52
		Female	199.1	2	3.82
Oregon	Reynolds 1978	Male	86	1	—
		Female	162	4	—
Oregon	Henny (In Reynolds 1978)	Male	96	4	—
		Female	177	5	—
Wisconsin	Mueller and Berger 1970	Male	100	899	—
		Female	170	1009	—
Northeast U.S.	Storer 1966	Male	99	—	—
		Female	177	—	—
Northcentral U.S.	Craighead and Craighead 1956	Male	102	98	—
		Female	179	92	—

This habitat type corresponds to the "mixed deciduous-coniferous forest" of Kessel (1979) and the "closed, mixed conifer and deciduous forest" of Viereck et al. (1982). Nests were usually built in white spruces, which were scattered singly or in small stands throughout the matrix of deciduous trees.

I. BREEDING BIOLOGY

Of the 19 active nests located, 2 were observed from the time the birds arrived until they and their offspring dispersed from the nest sites. Three nests were discovered during the egg-laying phase, six during incubation, four during the nestling period and one during the fledgling phase. Three nests were found after hawks had dispersed.

BREEDING BIRDS

Spring Arrival. Arrival of sharp-shinned hawks coincides with the arrival of avian prey (B. Kessel unpubl. data 1952-1982). I saw sharp-shinned hawks as early as 10 May in 1979 and 1 May in 1980 and in both instances, prey species had been present for at least a week before the hawks were seen. B. Kessel (unpubl. data 1952-1982) reports 29 April as the earliest sharp-shin arrival date, but R. B. Weeden (pers. comm.) saw one on 20 April 1980 and D. P. Pengilly and R. H. Meehan (pers. comm.) saw two near Fairbanks on 25 April 1979.

Courtship and Pairing. Although I heard courtship displays frequently, they were brief, and I saw them clearly only three times. Display consisted of a male flying in broad circles just above the

treetops with tail closed and undertail coverts flared, uttering a nasal "peee-peee-peee" call. At three nests, aerial display occurred over the nest site. At the two nests observed from arrival, courtship behavior was evident at first sighting and continued until first eggs were laid.

The male at the Chena 1980 nest site was never seen or heard displaying. The first time this site was known to be occupied in 1980 was 1 May, when two hawks were seen perching together. This was before droppings or prey remains were found, implying, perhaps, that the birds were paired when they arrived at the nest site.

I saw a male in late May 1982 flying and calling as above, except that he moved at least 2 km during his display. He frequently dove steeply, quickly regained his original altitude and resumed circling. I assumed that this was an unpaired bird trying to attract a female.

I heard vocalizations characteristic of copulation (Shelley, In Bent 1937) on three separate occasions at two nest sites, but I never saw birds copulate.

Age of Breeding Birds. Pairings between birds in adult plumage were most common (Table 4). However, 6 of 14 females (42.9%) were in brown immature plumage. Only 1 of 14 males (7.1%) was "immature".

Hawks breeding in immature plumage have been noted previously (Hennessy 1978). There are several possible explanations for this. If foraging experience is indeed a prerequisite for successful nesting (Newton 1979), we would expect most breeding males to be adults, since

Table 4. Age of sharp-shinned hawks breeding in interior Alaska, 1978-1981.

Male x Female	Number of Pairs (%)
Adult[1] x Adult	8 (57.1)
Adult x Yearling[2]	5 (35.7)
Yearling x Adult	0 (0.0)
Yearling x Yearling	1 (7.1)
Total	14 (99.9)

[1] adult-plumaged bird

[2] brown- (immature-) plumaged bird

they provide the greater part of their families' food and their experience would allow them to concentrate on providing food while yearlings would still be learning the necessary skills. Newton (1979) suggests that many male hawks are physiologically unable to breed in their first year. We would also expect that more adult than "immature" females would breed, because there ought to be more adults than "immatures" present since these birds live tor up to six years (USFWS Bird Banding Laboratory unpubl. data). A large proportion of immatures breeding might indicate high adult mortality (Brown 1976). Conversely, McGowan (1975) reported that high proportions of female goshawks breeding in immature plumage indicated favorable conditions and a. rapidly-expanding goshawk population. This complex issue warrants further investigation.

Newton et al. (1981) reported that among sparrowhawks (Accipiter nisus), adult-adult and yearling-yearling matings were more frequent, and adult-yearling matings less frequent than would be expected if mating were random with respect to age, a tendency not evident in this study (Table 4). Adult sparrowhawks produced larger clutches and larger broods than did yearlings (Newton et al. 1979, 1981), a trend not clearly evident in sharp-shinned hawks in Alaska (Table 5).

Molt of Breeding Birds. In the annual molt, primaries were replaced from the innermost outwards. Typically, when one feather was about half-grown, the adjacent one was molted. After the first few primaries were molted, replacement of both secondaries and retrices

Table 5. Clutch sizes, numbers of eggs hatched, and numbers of nest-
lings rledged for pairs of known-age sharp-shinned hawks,
interior Alaska, 1978-1981.

Male x remale	Clutch Size (n, S.D.)	# Hatched (n, S.D.)	# Fledged (n, S.D.)
Adult x Adult	5.33 (3, 0.58)	4.75 (8, 1.04)	2.4 (5, 1.82)
Adult x Yearling	5.0 (4, 0.82)	3.6 (5, 1.82)	2.0 (4, 1.83)
Yearling x Yearling	no data	5.0 (1, 0)	5.0 (1, 0)

began. The outermost secondary was molted first, but subsequent
molting of reathers was irregular. Thus, hawks sometimes had two or
three gaps in the secondaries. The central pair of retrices was
usually the first to be molted, followed by the outermost. Thereafter,
molt was irregular. Typically, growing retrices were supported by at
least one adjacent fully-grown feather. Newton and Marquiss´ (1982b)
detailed observations of molt in sparrowhawks are generally applicable
to sharp-shinned hawks in this study.

In females, molt began prior to nest construction and proceeded
rapidly. In two birds, 80% of flight feathers were fully replaced by
the mid-nestling period. Newton and Marquiss (1982b) documented an
arrest in the molt of female sparrowhawks mid-way through the breeding
season. A similar arrest appeared to be present in female sharp-
shinned hawks, but molted feathers were less evident because females
began spending time away from nests at that time, so positive evidence
is lacking.

Molt in males began about the time of egg-laying and progressed
more slowly than in females. Males retained a nearly full complement
of rlight reathers during periods when they were sole providers of food
for remales and nestlings. By the mid-nestling period, two males were
less than half as far along in the molt as their mates. Platt (1973)
reported that a male sharp-shinned hawk showed no signs of molt until
the young were one week old, about the time his mate´s molt was ar-
rested. I saw no pairs in which both birds were simultaneously in

heavy molt.

At two nests, I found large fragments of tarsal scales, implying that the keratinized epidermis of the legs and feet is also replaced regularly.

NESTING

Nest Site Selection and Nest Area Tenacity. Sharp-shinned hawks frequently used past nesting areas. The reoccupancy rates for sharp-shinned hawks in interior Alaska was 0.33 (Table 6), nearly twice the rate of 0.18 reported by Reynolds and Wight (1978) for sharp-shinned hawks in Oregon.

Two cases suggest that individual hawks returned to specific nest areas:

1) An adult male, trapped and banded 200 m from the Campus 1978 nest, was not the Campus 1978 male. He was recovered the following year 2 km from the Campus site at the Backyard 1979 nest, where he had paired with a yearling female. While he may not have been one of the pair occupying the Backyard site in 1978, it is certain that he returned in 1979 to within 2 km of where he was trapped in 1978.

2) Comparison of color banding patterns of molted feathers (Opdam and Müskens 1976) collected in three consecutive years at the Chena area suggested that the same male had occupied the area each year. Also, during all 3 seasons of investigation at the Chena area, I collected 37 intact heads of avian prey from plucking perches, a peculiarity in prey handling not found elsewhere.

Table 6. Nest area tenacity of sharp-shinned hawks, interior Alaska, 1978-1981.

| | Number of Years of Occupancy | | | | | |
	1	2	3	4	R/R^2	Reoccupancy Rate
Number of Nest Areas Revisited	-	6	5	4	5/15	0.33
Number of Nest Areas Reoccupied	6^1	3	1	1		
% Reoccupancy	-	50	20	25		

[1]Number of nest areas occupied for one year only.

[2]Number of nest areas reoccupied/number of nest areas revisited.

<u>Nest Site Vegetation</u>. Vegetation at nest sites was extremely dense (Table 7). Tree species near sharp-shinned hawk nests were paper birch (<u>Betula papyrifera</u>), white spruce (<u>Picea glauca</u>), black spruce (<u>P</u>. <u>mariana</u>), quaking aspen (<u>Populus tremuloides</u>), green alder (<u>Alnus crispa</u>) and several species of willow (<u>Salix</u> spp.), although not all sites included individuals of each of these species. The understory consisted of younger individuals of these tree species, along with perennial shrubs (high bushcranberry <u>Viburnum edule</u>, cranberry <u>V</u>. <u>vitis-idaea</u>, blueberry <u>Vaccinium uliginosum</u>, rose <u>Rosa acicularis</u>, Labrador tea <u>Ledum groenlandicum</u>, seasonal growth of horsetail <u>Equisetum sylvaticum</u>, bunchberry <u>Cornus canadensis</u>, herbs and grasses, and mosses and lichens. Cover by canopy and ground vegetation was moderate to complete (Table 7).

Trees at nest sites were relatively young (Tables 8 and 9), with older individuals interspersed occasionally.

Growth form of trees, rather than age, may be a more reliable parameter by which to characterize nest sites. Age of nest tree ($\overline{X}$ = 36.1 years, SD = 21.7, n = 11) was more variable than DBH ($\overline{X}$ = 0.183 m, SD = 0.096 m, n = 26). Using the growth form nomenclature of James and Shugart (1970), nest sites were dominated by class A trees (7.5 - 15 cm DBH), with decreasing numbers of B (15 - 22.5 cm DBH), C (22.5 - 37.5 cm DBH), D (37.5 - 52.5 cm DBH), and E (52.5 - 67.5 cm DBH) class individuals interspersed (Table 10).

Successionally speaking, typical sharp-shinned hawk habitat occurs

Table 7. Vegetation density at eighteen sharp-shinned hawk nest sites, interior Alaska, 1978-1981.

	Trees per 0.04 ha Plots	Trees per ha	Shrubs per ha	Canopy Cover (% of Sky Obscured by Vegetation)	Maximum Canopy Height(m)	Ground Cover (% of Ground Obscured by Vegetation)
$\bar{x}$	91.4	2286.1	8251.1	87.5	16.6	70.8
SD	20.69	517.15	2941.81	9.12	2.55	20.95
Max	137	3425	14240	100	22.9	100
Min	51	1275	5400	60	13.4	30

Table 8. Age of trees at sharp-shinned hawk nest sites, interior Alaska, 1978-1981.

Species	Tree Size Class (James and Shugart 1970) A	B	C	D
white spruce				
$\bar{X}$	36.3	39.4	47.0	--
SD	5.47	2.23	2.83	--
Max	48	43	49	--
Min	31	37	45	--
n	8	7	2	--
n sites	3	3	1	
paper birch				
$\bar{X}$	36.4	42.5	--	--
SD	4.11	5.09	--	--
Max	45	52	--	--
Min	31	38	--	--
n	17	6	--	--
n sites	4	4	--	--
quaking aspen				
$\bar{X}$	--	50.7	--	--
SD	--	3.82	--	--
Max	--	57	--	--
Min	--	46	--	--
n	--	7	--	--
n sites	--	2	--	--
green alder				
$\bar{X}$	28	--	--	--
SD	0.0	--	--	--
Max	28	--	--	--
Min	28	--	--	--
n	1	--	--	--
n sites	1	--	--	--
nest trees (white spruce)				
$\bar{X}$	35	40	49	87
SD	2.58	4.57	0.0	0.0
Max	36	49	49	87
Min	32	34	49	87
n	4	8	1	1

Table 9. Characteristics of sharp-shinned hawk nest trees,
interior Alaska, 1978-1981.

		Single Nest Trees	Multiple Nest Trees	Total for All Trees
Age (years)	$\bar{X}$	49	36.1	42.6
	SD	17.6	2.5	13.8
	Max	87	39	87
	Min	34	32	32
	n	7	7	14
Height (m)	$\bar{X}$	14.5	13.5	14.2
	SD	3.5	1.8	3.1
	Max	19.8	16.8	19.8
	Min	10.7	11.6	10.7
	n	13	7	20
Height of Nest (m)	$\bar{X}$	6.7	6.9	6.8
	SD	1.6	1.6	1.6
	Max	10.5	8.7	10.5
	Min	4.5	4.9	4.5
	n	13	4	17
Diameter at Breast Height (m)	$\bar{X}$	0.248	0.110	0.182
	SD	0.084	0.048	0.097
	Max	0.388	0.204	0.388
	Min	0.162	0.040	0.040
	n	13	12	25

Table 10. Vegetation characteristics of
          Alaska, 19/8-1981.

		paper birch	white spruce
Class A Trees			
(7.5-15 cm DBH)			
	$\overline{X}$	43.4	13.9
	SD	30.80	10.24
% of Class Total		53.8	17.2
% of Overall Total		47.4	15.2
	Max	103	41
	Min	5	3
Class B Trees			
(15-22.5 cm DBH)			
	$\overline{X}$	3.8	3.7
	SD	4.45	3.18
% of Class Total		41.8	40.7
% of Overall Total		4.1	4.0
	Max	12	13
	Min	0	0
Class C Trees			
(22.5-37.5 cm DBH)			
	X	1.1	0.4
	SD	1.51	0.61
% of Class Total		64.7	23.5
% of Overall Total		1.2	0.4
	Max	5	2
	Min	0	0

Trees per 0.04 ha Plot					
willow	dead tree	black spruce	green alder	quaking aspen	TOTAL
13.8	3.2	2.3	2.2	1.7	80.5
13.36	4.19	7.94	4.16	4.69	
17.1	4.0	2.9	2.7	2.1	99.8
15.1	3.5	2.5	2.4	1.9	88.0
41	16	33	14	20	133
0	0	0	0	0	28
0.7	0.1	0.4	–	0.4	9.1
1.68	0.24	1.65	–	1.25	
7.7	1.1	4.4	–	4.4	100.1
0.8	0.1	0.4	–	0.4	9.9
7	1	7	–	5	18
0	0	0	–	0	0
0.1	0.1	–	–	–	1.7
0.47	0.24	–	–	–	
5.9	5.9	–	–	–	100.0
0.1	0.1	–	–	–	1.8
2	1	–	–	–	6
0	0	–	–	–	0

Table 10. (continued)

	paper birch	white spruce	willow	dead tree	black spruce	green alder	quaking aspen	TOTAL
Trees per 0.04 ha Plot								
Class D Trees								
(37.5-52.5 cm DBH)								
$\overline{X}$	–	0.2	–	–	–	–	–	0.2
SD	–	0.51	–	–	–	–	–	
% of Class Total	–	100.0	–	–	–	–	–	100.0
% of Overall Total	–	0.2	–	–	–	–	–	0.2
Max	–	2	–	–	–	–	–	2
Min	–	0	–	–	–	–	–	0
Class E Trees								
(52.5-67.5 cm DBH)								
$\overline{X}$	–	0.1	–	–	–	–	–	0.1
SD	–	0.24	–	–	–	–	–	
% of Class Total	–	100.0	–	–	–	–	–	100.0
% of Overall Total	–	0.1	–	–	–	–	–	0.1
Max	–	1	–	–	–	–	–	1
Min	–	0	–	–	–	–	–	0
Total Trees per Plot	48.3	18.3	14.6	3.4	2.7	2.2	1.7	91.2
% of Total	52.8	20.0	16.0	3.7	3.0	2.4	1.9	99.8

– none present

relatively briefly in interior Alaska (Foote 1983). The most likely factor preventing sharp-shinned hawks from extensively using more advanced seral stages is low prey availability. The abundance and variety of prey found in the diverse, highly-incised, three-dimensional nesting habitat preferred by sharp-shinned hawks simply does not exist in older successional stages (Spindler and Kessel 1980). Several nest sites demonstrated that sparse canopy or ground cover, old stands of trees, a lack of suitable plucking perches or even a combination of these could be tolerated, but low abundance and variety of prey would present a more difficult problem. In interior Alaska, frequent wildfires set back the successional process, and this may, ultimately, be the most important factor influencing sharp-shinned hawk distribution and abundance.

Conversely, prevention and suppression of fire may have important and deleterious effects on sharp-shinned hawk populations in Alaska in the future. Growing human populations will demand greater suppression of wildfire, with the resultant climax plant communities being unsuitable for sharp-shinned hawk breeding. Just as large scale agricultural, residental and industrial development have significantly altered raptor habitat in the 48 contiguous states, fire suppression accompanying other development may have a significant impact on sharp-shins in Alaska.

Nest Trees. Of 19 active nests, 18 were in white spruce trees. Fifteen were in single trees and three were built between the trucks

of two or three closely-situated trees. One nest was constructed between the trunks of a clump of five small black spruce.

Single nest trees were older, taller and larger in diameter than multiple nest trees (Table 9). Nests in single trees were usually about halfway up the trunk, while nests between two or more trees were built higher in the trees and slightly further from the ground. All nests were within the forest canopy. Thirteen of fifteen (87%) single-tree nests were built against tree trunks, but two of four (50%) multiple-tree nests were not in contact with trunks. Live branches were present above and below all nests. Nests tended to be built on the southerly half of nest tree trunks ($0.05 > p > 0.01$) (Figures 1 and 2).

Nest trees were located on gentle to moderate slopes or on level spots on slopes (Figure 3). The slope gradient at nest sites ranged from 0% to 25% ($\bar{X} = 6.7\%$, SD = 7.10, n = 19). The fifteen nests on slopes were distributed randomly with respect to slope direction ($p < 0.20$) (Figure 2), but this should not be taken to imply that sharp-shinned hawk nests are built on all aspects. Vegetation type is probably more influential in nest site selection than slope direction alone, but, of course, the two are inextricably related.

Elevation, measured at the bases of nest trees, ranged from 152 m to 366 m, mean sea level ($\bar{X} = 240$ m, SD = 74.3 m, n = 19). Multiple-tree nests occurred at lower elevations ($\bar{X} = 165$ m, SD = 14 m, n = 4) than single tree nests ($\bar{X} = 260$ m, SD = 70.8 m, n = 15). This reflects, perhaps, the moister, cooler conditions at lower elevations,

NORTH

NW   NE

WEST   TREE
              TRUNK   EAST

SW   SE

SOUTH
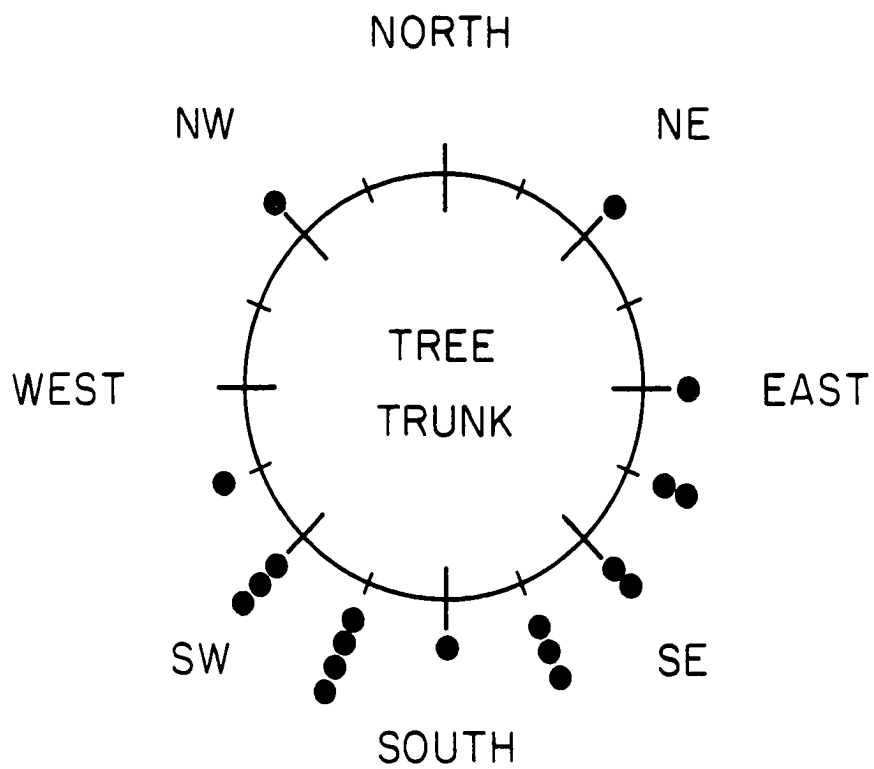
Figure 1. Directional exposure of sharp-shinned hawk nests,
           interior Alaska, 1978-1981.
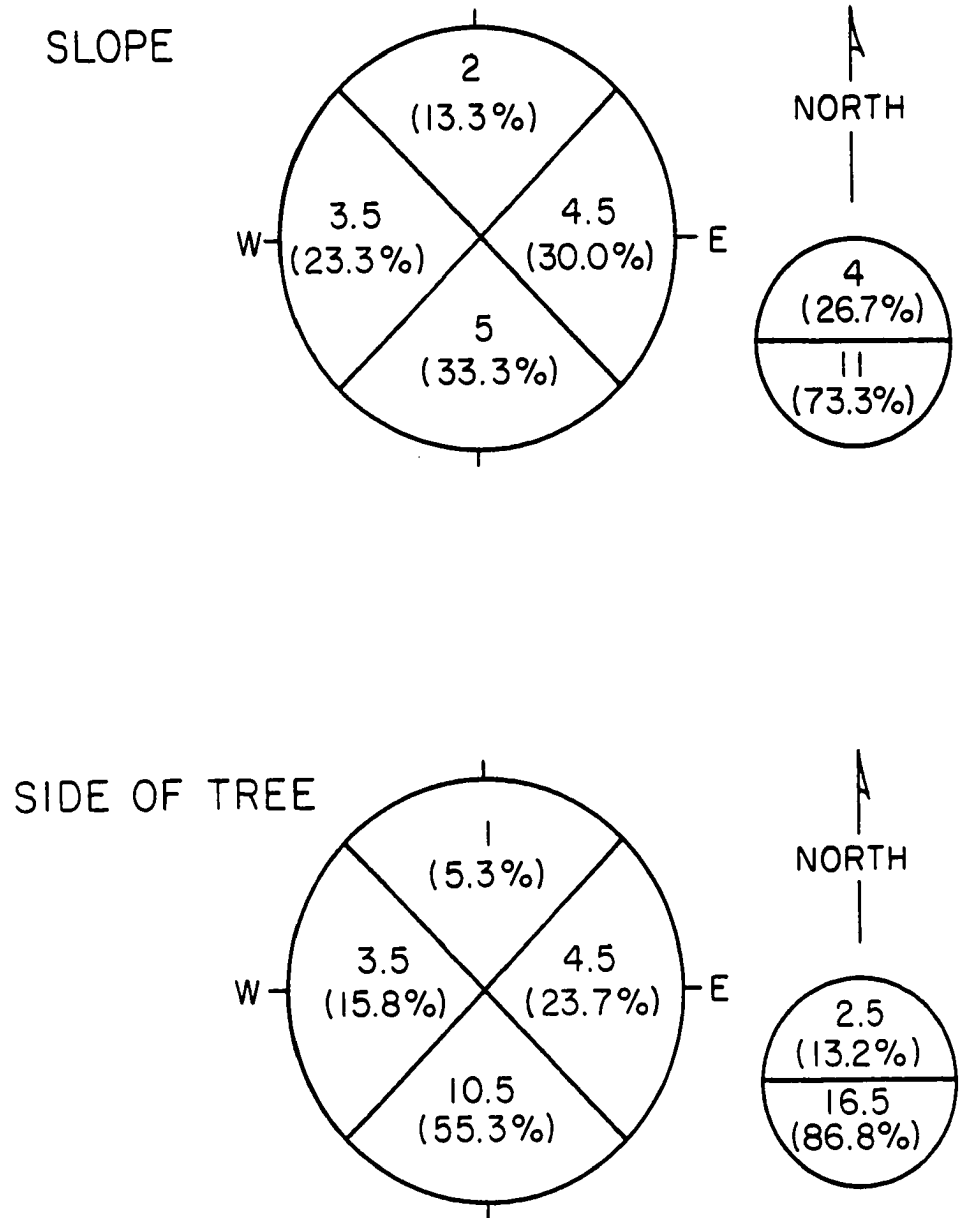
Figure 2. Distribution of directional exposure of sharp-shinned hawk nest site slopes and nests, interior Alaska, 1978-1981.

NORTH

NW ● NE

WEST EAST

SW SE

SOUTH

● On slope, n=13 (68.4%)

○ Level spot on slope, n=2 (10.5%)

◎ Level ground or hilltop, n=4 (21.1%)
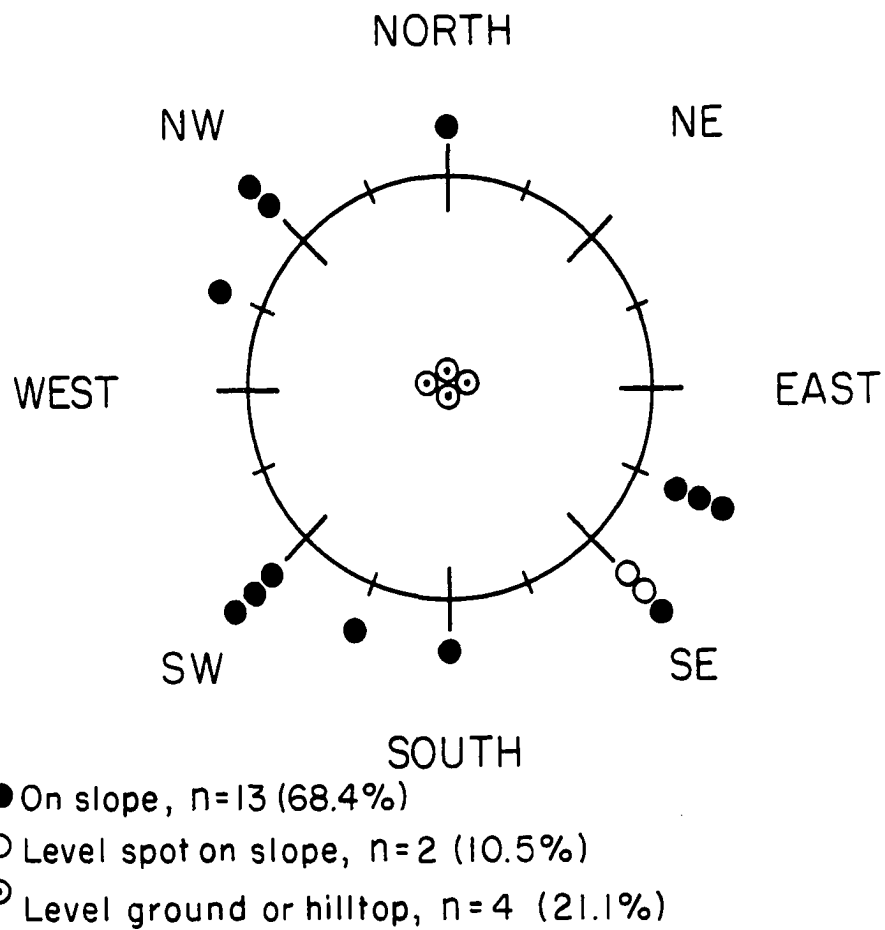
Figure 3. Directional exposure of sharp-shinned hawk nest site slopes, interior Alaska, 1978-1981.

which result in shorter, bushier, more closely-spaced trees, rather than an active process by which birds seek out multiple-tree nesting situations.

Nests and Nest Construction. Nests were large, bulky platforms of white spruce and paper birch twigs. Often, aspen, willow and tamarack twigs were also present. Nests were roughly circular about 0.5 m in diameter and 0.2 m thick. Nests in single trees were slightly larger than those in multiple trees (Table 11). A shallow cup, almost always present, was occasionally lined with flakes of dry aspen, spruce or willow bark.

As with many other raptors, the nests of sharp-shinned hawks are large, simple structures. Nests must be large to accomodate five or six rapidly-growing young sharp-shins, and there seems to be little need for complex nests, since nest trees provide excellent protection and concealment. Simple nests may also indicate that the sharp-shinned hawk adaptive strategy has placed little emphasis on the ability to modify the nesting environment.

I collected and dissected the Melchior 1981 nest and found 769 twigs, although a few were lost when the nest was removed from the tree. This nest, 0.43 m x 0.61 m x 0.25 m, was larger than the mean for 17 nests, 0.489 m x 0.516 m x 0.211 m, so the typical nest would contain fewer twigs, perhaps about 600.

Construction was shared by the sexes, but females contributed the great majority of the material at two nests, implying large energy

Table 11. Dimensions of sharp-shinned hawk nests, interior
Alaska, 1978-1981.

		Axial Width (m)	Radial Width (m)	Depth (m)	Cup Depth (m)
Single	X̄	0.496	0.533	0.201	0.034
Nest	SD	0.1151	0.1112	0.0528	0.0154
Trees	Max	0.71	0.69	0.28	0.051
	Min	0.33	0.38	0.13	0.0
	n	14	14	14	13
Multiple	X̄	0.457	0.440	0.203	0.037
Nest	SD	0.1779	0.0173	0.0377	0.0169
Trees	Max	0.66	0.46	0.23	0.051
	Min	0.33	0.43	0.15	0.019
	n	3	3	4	4
Total	X̄	0.489	0.516	0.201	0.034
	SD	0.1223	0.1069	0.0489	0.0152
	Max	0.71	0.69	0.28	0.051
	Min	0.33	0.38	0.13	0.0
	n	17	17	18	17

expenditures by females during nest-building. Of 31 deliveries of nest material observed, only two were by males, and in each instance, the twigs bought by males were quite small compared to those the females brought. On two occasions, I saw the Campus 1978 female hurl herself into the branches of a white spruce, jumping on and pulling at several dead twigs. When she finally broke twigs free, she returned to the nest, carrying single twigs in her beak, and added them to the structure. Twigs were added sporadically for several days after the main platform was in place. I saw the Campus 1978 female add several twigs to the nest late in the nestling period.

Only four of 19 nests studied were built between the trunks of two or more closely-spaced trees, yet three of those four were at the Chena area. Females were different individuals in 1978 and 1980, and were probably different each year. I suspect that the male at the Chena area was the same individual each year (see Nest Site Selection and Tenacity). Thus, the Chena male, whose presence was the only apparent constant at the area from year to year, may have selected these atypical nest locations.

Nests were built in a suprisingly short period of time. There was no new nest at the Chena area the evening of 7 May 1979, but a new nest was complete the evening of 11 May 1979. Field observations indicated that sharp-shinned hawks were not active through the semi-darkness of the Alaskan night, so they must have delivered a great number of twigs in about 65 hours. Locating, securing, retrieving and incorporating

into a nest some 600 twigs constitutes a substantial energy expenditure. Rawson (In Bent 1937) noted a case of even faster nest construction; a new nest was built in just one day after the original was destroyea. Considering their manner of obtaining these twigs and that this endeavor comes between the energetic drain of migration and the stresses of egg-laying and molt, this achievement is all the more remarkable.

Nests were rarely reused, but reoccupation of nest areas was common. One nest, at least three years old, was re-used in 1980. Platt (1976) found only one instance of re-use in 61 nestings (1.6%). However, in this study, eight of ten (80%) nest areas contained old nests when first discovered, and seventeen of nineteen (89.5%) active nests were built within 100 m of an old nest. Perhaps old nests provide important visual cues, encouraging sharp-shinned hawks to nest in the vicinity.

Certainly, the hawks must select a place with a sturdy framework for nest construction, but they seem as well to actively seek out a place that is both protected from the elements and concealed from enemies. Nest trees shield nests and young very effectively from wind and rain. Nests are well-protected from the elements, and inactive nests persist for many years. I found 17 inactive nests within 100 m of the Banner Creek 1978 nest. Nests are remarkably well-concealed, and I had great difficulty locating them. Presumably, predators and other potential enemies would also have difficulty detecting sharp-

shinned hawk nests.

Branches tended to be denser and more numerous on the south sides of nest trees. Conceivably, it is easier for hawks to construct a stable nest platform across the stouter, less widely divergent branches of the southern aspects of trees. Dense, overhanging branches might shade nests from hot sunlight as suggested by Reynolds et al. (1982) for accipiters in Oregon, but a more plausible explanation for nests at high latitudes is that nests on the southern sides of trees are more fully exposed to the warmth of the early-morning sun (K. Tuttle, In McElroy 1977). One might suspect that if the hawks cannot tolerate high temperatures and direct sunlight, they would also select nest sites on north- and east-facing slopes (Reynolds et al. 1982), but in interior Alaska, where the summer sun rises far to the northeast and circles round to set in the far northwest, preference for slope direction was neither expected nor observed. Again, vegetation, especially on north-facing slopes, may not be appropriate for nesting and this probably exerts a stronger influence on nest site selection than does how intensely the sun strikes the site.

Other Nest Site Characteristics. Nest sites usually contained one major plucking perch and several auxiliary plucking perches. Prey was usually plucked on clumps of willows, dead and bent toward or actually lying on the ground, sometimes on mossy stumps or fallen logs, and rarely on low, live branches of spruce trees. Plucking perches were within 50 m of nest trees, and were level with or uphill from nests.

At tour nest areas which were used for two or more seasons, sharp-shinned hawks used the same plucking perches from year to year. This may indicate that suitable plucking perches are at a premium, a factor which may influence selection of nest sites by the hawks.

Twelve of nineteen (63%) nests were within 20 m of paths, trails, old roads or large natural spaces in the foliage, and all were within 50 m ot such features. This phenomenon has been noted in accipiters by many other authors (e.g., Bent 1937, Beebe 1974 and 1976, Tuttle In McElroy 1977, Lee 1981). Also, plucking perches were usually connected with nests by breaks in understory vegetation. It can be assumed that it is less energetically expensive to fly directly from one point to another than it is to manuever through dense vegetation, yet this does not necessarily imply that sharp-shinned hawks intentionally build their nests near breaks in vegetation. It is, I think, equally probable that nests are near paths and trails because it is easier for investigators to travel along such open areas, and naturally, the nests they tind are close to these thoroughfares. I suspect that wherever a sharp-shinned hawk might nest in interior Alaska, it would be able to tind and utilize a "flight-path" relatively free of foliage.

TERRITORY AND HOME RANGE

Territoriality and Nest Site Defense. Intensity of nest site defense varied widely among the birds I observed. Some birds left quietly when observers approached, but others attacked energetically. Some attacked intruders up to 60 m from the nest, while others waited

until interlopers actually contacted the nest tree before reacting. Generally, males defended with greater determination than females, especially early in the breeding season, when females maintained incubation or brooding through most disruptions. As nestlings grew, so did both parents' defense reaction against intruders. By the late nestling period, most parents attacked enemies enthusiastically, although the males remained the most determined defenders.

Frequent vocalization, a harsh "keuk-keuk-keuk", accompanied diving attacks. Hawks struck me repeatedly on the head, shoulders and back when they could approach from behind; if I faced the birds, they usually flared away before making contact. At the Chena 1978 and 1979 nests, I was often struck by both male and female, in quick succession and from different directions. Once, as I sat measuring nestlings from the Backyard 1979 nest, the adult male struck me squarely in the left ear while holding a partially plucked juvenile dark-eyed junco (_Junco hyemalis_), which he dropped on impact. Later that year, I was struck by an unplucked immature yellow warbler (_Dendroica petechia_) dropped by the Dogpatch male as he flew over.

In interspecific encounters, sharp-shinned hawks followed one of three avenues:

1) animals smaller or weaker than themselves were killed and eaten,

2) larger animals were harassed, and

3) larger animals that posed a potential threat were avoided.

I saw one silent attack on a full-grown domestic short-haired cat (<u>Felis</u> <u>catus</u>), which was carrying a dead northern red-backed vole (<u>Clethrionomys</u> <u>rutilus</u>) past the Campus 1978 nest tree. The male struck it sharply on the left flank, whereupon the cat dropped the vole and left the area. I observed eleven attacks (six by the female, four by the male and one by both) on a red squirrel (<u>Tamiasciurus</u> <u>hudsonicus</u>) whose midden lay directly beneath the flight path from the Campus 1978 nest to the major plucking perch. Most attacks resulted in rolling and struggling on the ground, and while the hawks were silent, the squirrel was very vocal. Once, the female struck the squirrel on the ground and held on as it ran to a large white spruce and circled up the trunk. She released her grip only after three complete circuits of the tree's circumference, continued the pursuit on the wing, then abandoned the chase when the squirrel reached dense branches 10 m from the ground. The squirrel's apparent attempt to approach the nest tree precipitated some attacks, but several, including the one described above, seemed entirely unprovoked.

I also observed attacks on two red-tailed hawks (<u>Buteo</u> <u>jamaicensis</u>), a golden eagle (<u>Aquila</u> <u>chrysaetos</u>), a bald eagle (<u>Haliaetus</u> <u>leucocephalus</u>), and two great horned owls (<u>Bubo</u> <u>virginianus</u>). These large raptors were harassed in flight wherever they were encountered, but assaults on non-prey mammals were observed only near nests.

Sharp-shinned hawks have been known to attack a wide variety of animals, including meadowlarks (Bent 1937), belted kingfishers (<u>Ceryle</u>

alcyon) (Skinner 1928, McCabe and McCabe 1928), mourning doves (Zenaida
macroura) (Madson 1978), northern bobwhites (Colinus virginianus) (Bent
1937), pileated woodpecker (Dryocopus pileatus) (Kilham 1958), night
herons (Bent 1937), gulls (Bent 1937), wood ducks (Aix sponsa) (Morris
1892), rock ptarmigan (Lagopus mutus) (D. J. Kelleyhouse via D. J. Ver-
nam pers. comm.), prairie falcons (Falco mexicanus) (Bent 1937),
domestic geese (D. G. Roseneau pers. comm.), gray squirrels (Sciurus
carolinensis) (Bent 1937), porcupines (Erethizon dorsatum) (Kelley and
Kelley 1969) and bobcats (Lynx rufus) (LaFave 1955). Most of these at-
tacks were probably defensive in nature, rather than predation at-
tempts.

Young sharp-shinned hawks are at times vulnerable to attack by
both avian and terrestrial predators, but adults would seem to have
very few natural enemies. In typical nesting habitat, adult sharp-
shins can outmanuever virtually any avian predator. typical nesting
habitat. Still, the Dogpatch 1980 female left the nest site quickly
and quietly when an immature male goshawk (Accipiter gentilis) came in-
to view. She made no attempt to drive the goshawk away, even though
it landed on the nest, which, at that time, contained four eggs.
Whether goshawks actually do prey upon sharp-shinned hawk eggs, young,
or adults is not known. L. G. Swartz (pers. comm.) found sharp-shinned
hawk remains in a peregrine falcon eyrie near the Yukon River, and R.
J. Ritchie (pers. comm.) saw a male sharp-shin narrowly escape the
simultaneous attack of three peregrines over the Tanana River.

Curiously, nesting sharp-shinned hawks consistently flew away quietly whenever I visited nest sites accompanied by my English springer spaniel.

Despite sharp-shinned hawks' usual intolerance of intruders near their nests, some nested where human activity presumably would be disruptive. I found nests near roads, parking lots and occupied houses. Construction of a house only 30 m from the Springer 1978 nest began during incubation and did not prevent that pair from fledging five young, although the site was vacant the following two seasons. Both members of the Springer 1978 pair were in immature plumage, a trend noted in accipiters that became habituated to human disturbance in Utah (Lee 1981). Perhaps lack of experience can be equated with "tameness".

Home Range Size. Radiolocations showed that the Backyard 1979 male was usually nearer the nest ($\bar{X}$ = 0.31 km, SD = 0.119 km, n = 6) than the female ($\bar{X}$ = 0.45 km, SD = 0.336 km, n=11) during the late nestling period (Figure 4). This is in direct contrast to the findings of other authors (Platt 1973, Newton 1978, Mueller et al. 1981), who reported that it was the female accipiter that "loitered" in the vicinity of the nest. A larger sample size may have shown the males's and female's hunting ranges to be more similar.

Estimated home range size was smaller than most of those reported by other investigators (Table 12).

Spacing of Nest Sites. Active nests were spaced quite regularly (Figure 5), and much more densely than was reported by Reynolds and
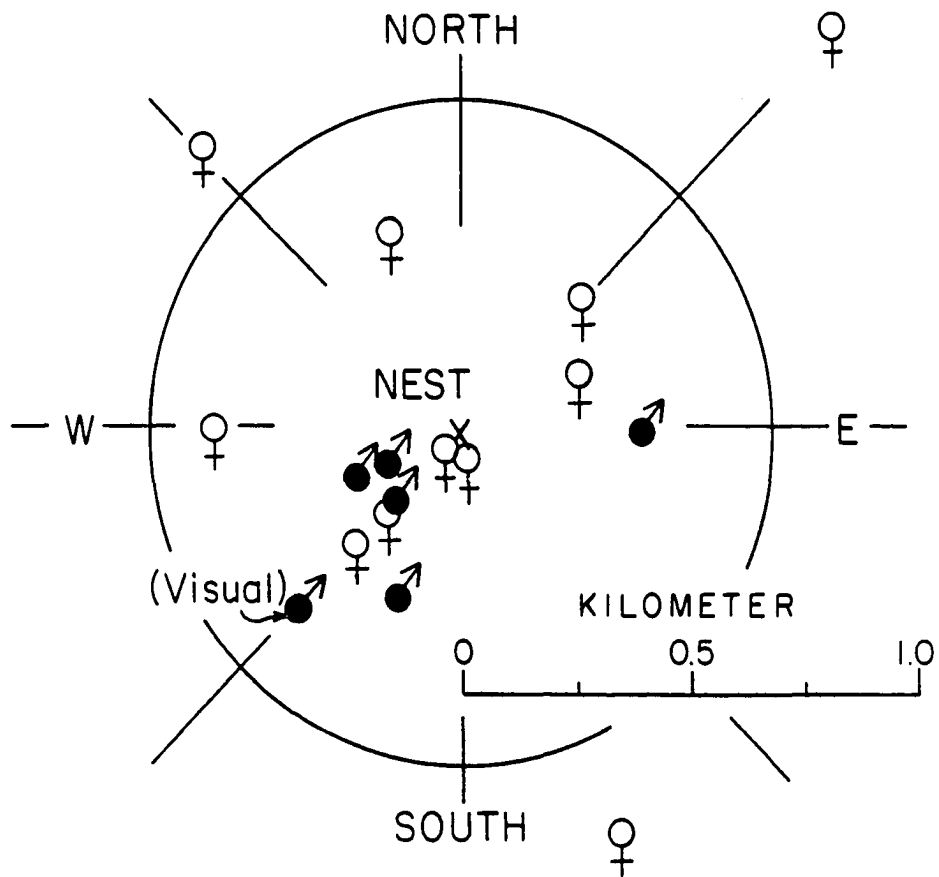
Figure 4. Radiolocations of a breeding pair of sharp-shinned hawks,
Backyard 1979 nest, interior Alaska.

Table 12. Home ranges of sharp-shinned hawks.

Location	Source	n	Radius of Movement (km)	Estimated Home Range Size (ha)
Alaska	This study	1	1.1	379.9
Ontario	Mueller et al. (1981)	1	1.5	706.5
Oregon	Reynolds (1978)	1 (?)	1.21	459.7
Wyoming	Craighead and Craighead (1956)	2	--	$100.1^{1}/1248.7^{2}$

[1] "observed"

[2] "maximum"

ACTIVE NESTS   WOODLAND
● 1978
○ 1979
▲ 1980
△ 1981
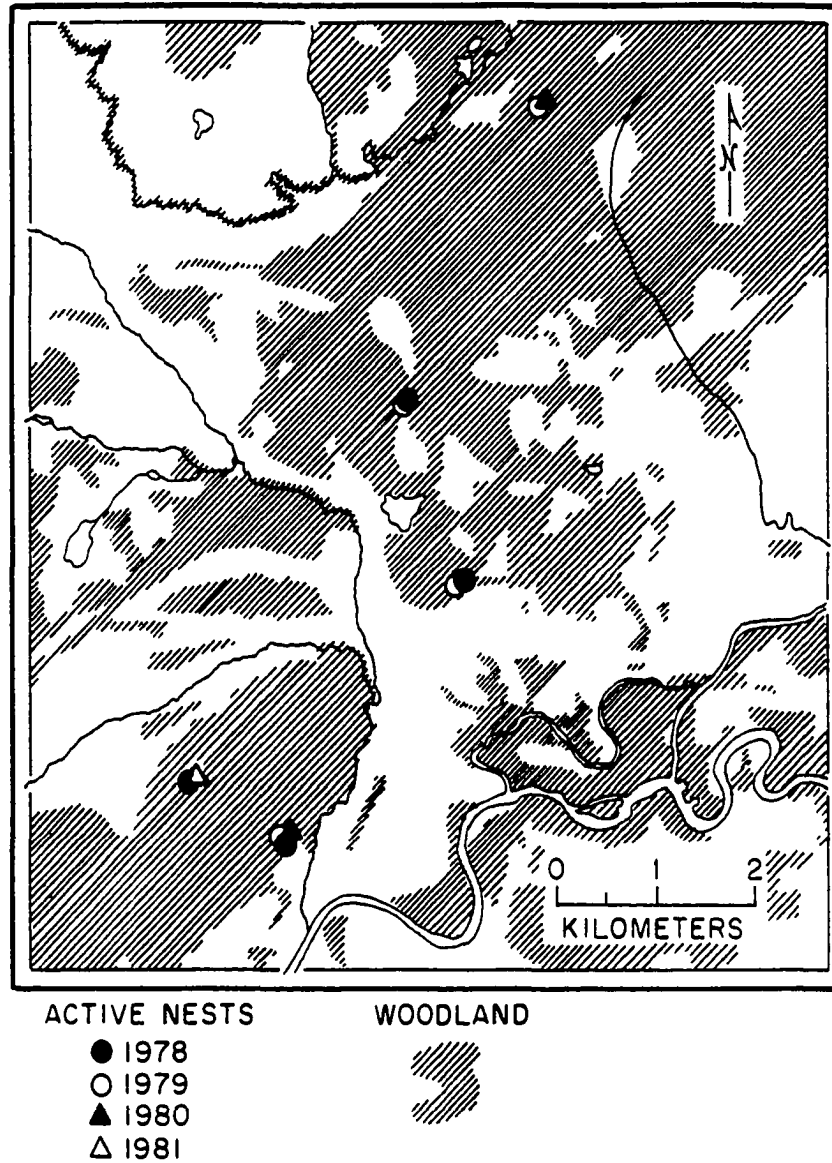
Figure 5. Spacing of sharp-shinned hawk nest sites, interior
Alaska, 1978-1981.

Wight (1978) for sharp-shinned hawks in Oregon (Table 13).

EGGS

Egg-laying. Data from five nests indicate that first eggs were laid as early as 14 May and as late as 27 May ($\bar{X}$ = 19 May, SD = 5.0, n = 5). At four nests, subsequent eggs appeared every other day, except for a 2-day gap between the appearance of the fifth and sixth eggs at the Dogpatch 1980 nest.

Eggs. Eggs observed in this study were as described by Bent (1937). Fifteen eggs were weighed at least twice during incubation in 1980. Eggs lost weight steadily, with a sharp loss just prior to hatching, presumably from loss of water after eggshells were pipped (Figure 6). Extrapolation of data indicated that eggs weighed 19-21 g when laid. Average egg weight at time of laying was estimated to be 20 g.

Twenty-six eggs were measured, six in 1979 and twenty in 1980. Alaskan eggs were larger than those measured by other investigators (Table 14). Beta-backscatter estimation of shell thickness of two addled eggs suggested that Alaskan shells were thicker than any measured in other studies (Table 14). I believe, however, that the contents of these eggs caused the device to register an exaggerated estimate of shell thickness. Backscatter analysis of three shell fragments gave similar figures to direct measurement of the same fragments. These apparently more reliable measurements showed Alaskan eggshells to be thinner than most other shells (Table 14). This indicates, per-

Table 13. Nesting density of sharp-shinned hawks.

| Source | Location | Year | Nearest-neighbor Distance (km) | | | | | Estimated Home Range (km^2) | Estimated Density (Pairs per 100 km^2) |
			$\bar{X}$	SD	Max	Min	n		
This Study	Alaska	1978	2.0	0.90	2.9	1.1	4	3.1	32.3
		1979	2.6	0.61	3.0	1.9	4	5.3	18.9
		Total	2.3	0.77	3.0	1.1	8	4.2	23.8
Reynolds and Wight (1978)	Oregon	1974	4.1	2.12	6.0	1.8	4	13.2	7.6
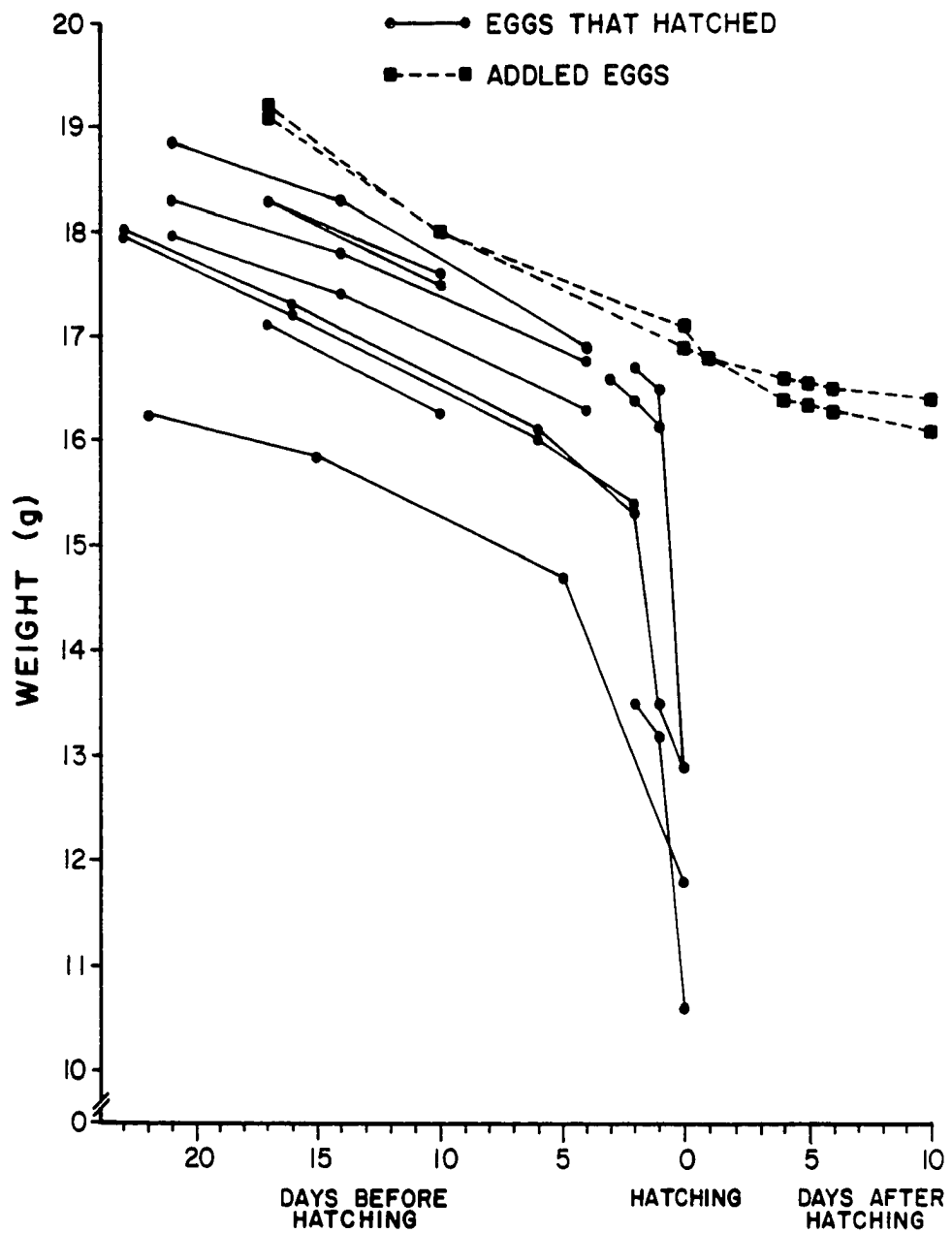
Figure 6. Weight loss in sharp-shinned hawk eggs, interior Alaska, 1979 and 1980.

Table 14. Measurements of sharp-shinned hawk eggs in mm.

Source	n	$\overline{X}$ Major Axis (SD)	$\overline{X}$ Minor Axis (SD)	Extremes	Thickness (SD)
This study					
Alaska					
whole eggs 1979-1980	26	38.80 (2.23)	30.75 (0.64)	<u>41.50</u> x <u>32.10</u> <u>29.95</u> x 30.50 36.10 x <u>29.55</u>	0.305 (0.01) (n=2)[1]
eggshell fragments 1978-1979	3	--	--	--	0.195 (0.02)[1] 0.214 (0.01)[2]
Western Foundation of					
Vertebrate Zoology 1875-1946	292	37.72 (1.39)	30.25 (0.73)	<u>42.58</u> x 31.05 <u>31.15</u> x 28.26 39.28 x <u>32.59</u> 35.20 x <u>28.00</u>	0.237 (0.02) (n=291)[2]
1958-1960	10	37.94 (2.52)	29.62 (1.51)	<u>41.00</u> x 30.40 <u>35.00</u> x <u>28.30</u> 38.73 x <u>32.06</u>	0.213 (0.02)[2]
Hennessy 1978	1	--	--	--	0.289 (0.00)
Anderson and Hickey 1972					
pre-1947	197	--	--	--	0.268 (0.004)[3]
1947-1958	4	--	--	--	0.245 (0.020)[3]

Table 14. (continued)

Source	n	$\overline{X}$ Major Axis (SD)	$\overline{X}$ Minor Axis (SD)	Extremes	Thickness (SD)
Sprunt 1955	?	36.83 (--)	29.21 (--)	--	--
Bent 1937	58	37.50 (--)	30.40 (--)	<u>40.60</u> x 30.50 <u>35.00</u> x 29.00 39.00 x <u>32.00</u> 36.60 x <u>28.90</u>	--
Bowles 1930	?	38.86 (--)	29.97 (--)	--	--
Rust 1914	5	37.90 (0.28)	33.58 (1.21)	<u>38.10</u> x <u>34.80</u> <u>37.59</u> x <u>31.75</u>	--

[1] estimated with beta-backscatter device
[2] measured directly on blown eggshells with modified bench caliper
[3] 95% confidence limit

haps, that Alaskan sharp-shinned hawks, like raptors elsewhere, have been adversely affected by environmental pollutants. On the other hand, larger clutch sizes (Table 15) may place a demand for calcium on females in excess of that for sharp-shins elsewhere, which could account for the thinness of Alaskan eggshells.

INCUBATION AND NESTLING PERIOD

Incubation. Incubation began when the last egg was laid, as early as 23 May and as late as 3 June ($\bar{X}$ = 28 May, SD = 3.8, n = 5). Incubation lasted 29-32 days ($\bar{X}$ = 30 days, SD = 1.7, n = 3).

Behavior of Adults. Incubation was carried out entirely by the female, who left the nest only to attack intruders or to eat. All prey was killed and delivered to plucking perches by the male. Food transfers occurred in a predictable sequence that persisted throughout the breeding season: the male arrived at the major plucking perch, usually within 50 m of the nest, and gave a "food announcement" call, a high-pitched "kee-kee-kee-kee-kee". The female responded with a "food begging" call, a series of plaintive, whining notes. She carefully raised herself from the eggs, moved to the edge of the nest and flew toward the male. Landing at or near the plucking perch, the female called more frequently; as the male plucked his prey, she called more "rapidly" until her vocalizations were nearly continual. Finally, the female rushed close and grabbed the prey, calling very "excitedly". At this, the male released the prey and flew a short distance away, uttering a rapid "chittering" cry as if agitated or annoyed. The female

Table 15. Mean clutch size, number of eggs hatched and number of young fledged per nest for sharp-shinned hawks in this study compared to others.

Place Year(s)	Source	Mean Number of Eggs per Clutch	Mean Number of Young per Nest	Hatching Success	Mean Number of Young Fledged per Nest	Fledging Success
Alaska 1979-1981	This study	5.1 (8)[1] (0.64)[2]	4.4 (14)[1] (1.40)[2]	82.9% (8)[1]	3.1 (14)[1] (1.86)[2]	79.4% (8)[1]
Wyoming 1975	Craighead and Mindell 1981	4.0 (2)	1.3 (2)	---	0.0	0.0% (2)
Oregon 1969-1974	Reynolds and Wight 1978	4.6 (5)	3.2 (5)	69.6% (5)	2.7 (11)	81.2% (5)
Wyoming 1949	Craighead and Craighead 1956	3.5 (2)	3.5 (2)	---	3.5 (2)	---

[1] Number of nests

[2] Standard deviation

either finished plucking the prey or began eating immediately; later
in the season, she carried the prey to the nest and fed the young.
This pattern is very similar to that described by Willoughby and Cade
(1964) for American kestrels (Falco sparverius).

I did not observe males hunting, but other investigators have
described hunting techniques (Bent 1937, Peeters 1961, Platt 1973, Wat-
tel 1973).

Males tended to gather more food than was required by the pair;
often, prey remains collected early in the season were nearly untouched
carcasses. Males spent much of their time perched near the nests, and
apparently hunted in the near vicinity, as it was exceedingly rare to
hear or see any prey animals within 100 m of the nests. Disappearance
of singing thrushes concurrent with appearance of thrush remains at
plucking perches suggests that males annihilated the local prey popula-
tion early in the season, but it is possible that prey animals learned
to avoid areas near nest sites, which would account for the lack of
prey near nest sites later in the season.

I found three large eggshell fragments on the ground up to 50 m
from three different nests, suggesting that nesting hawks, probably
females, carried empty shells away from nests and dropped them. I also
found seven castings containing eggshell fragments (Table 16), in-
dicating that some birds ingested eggshell fragments. Whether this was
intentional, as has been reported for other accipiters (Newton 1973,
Snyder et al. 1973), is not known.

Table 16. Contents of 2b7 sharp-shinned hawk castings, interior
Alaska, 1978-1981.

Material	Frequency of Occurrence	
	Number	% of Total
Feathers	263	98.5
Bird Bones	128	47.9
Bird Gizzards	23	8.6
Hair	15	5.6
Mammal Bones	5	1.8
Insect Parts	170	63.7
Spruce Needles	23	8.6
Plant Seeds	18	6.7
Eggshell Fragments	7	2.6
Twigs or Bracts	2	0.7

Throughout the nestling period, females tore prey into small pieces and distributed them suprisingly evenly among young. Pieces of prey refused by the nestlings were eaten by females, as were remnants of prey left over after young were satiated; these probably provided for all the food needs of females, which were seen eating away from the nest only twice during the nestling period. Females began leaving prey for the young to eat for themselves just prior to fledging and began eating alone and away from the nest.

When not brooding or feeding young, the adult female perched nearby. Once I saw a female shielding young from rain, but by the time that nestlings were apparently able to thermoregulate, females visited only to feed them. I did not observe females leaving nest sites to hunt, but twice observed them chasing and/or killing prey near nests.

I saw females swallow or carry away bones and legs of large prey birds, but saw no instances or evidence of removal of fecal matter or regurgitated castings.

Males hunted and perched near nests early in the nestling period. As nestlings grew, perching sites were further and further from the nest. Time spent within sight of nests decreased to nearly zero as nestlings approached fledging. Since I saw males only when they were delivering food, I could not tell how much time they spent perching or hunting.

The Campus 1978 male provided prey throughout the daylight hours, 0400-2200 AST, with slight increases late in the day and again early

the next morning (Figure 7); these increases in prey delivery acted to offset the effects of the nightly fast. The number of daily prey deliveries was relatively constant through the summer (Table 17), which is consistent with theories that accipiters supply food at a rate determined by hunting success and not the needs of the young (Newton 1978, Perrins and Geer 1980, Geer 1981). I did not determine hunting success through the summer, but noted no significant increases of prey delivery to young as they grew older and required more food (Table 17). I saw males deliver prey to nests on five occasions, and only once, during the late nestling period, did I see a male feeding the young.

When the young birds could tear prey on their own, parents often merely left food at the nest and departed quickly, usually retreating to a nearby perch after leaving prey. Similar "dumping" of prey by sparrowhawks was characteristic of birds facing a food shortage, i.e., they "dump" prey and hurry off to hunt for more (Newton 1978). Both Newton (1978, sparrowhawks), and Mueller et al. (1981, sharp-shinned hawks) hypothesized that females do not hunt extensively unless a shortage of prey reduces the male's success. The behavior of sharp-shinned hawks in this study suggests that there was no severe shortage of prey. Rather, prey was "dumped" at nests so parents could avoid being mobbed by the nestlings.

Hatching. Eggs hatched as early as 22 June and as late as 4 July ($\overline{X}$ = 27 June, SD = 3.4, n = 9). At each of fourteen nests, the entire clutch hatched in the same 24-hour period. At two nests, both with
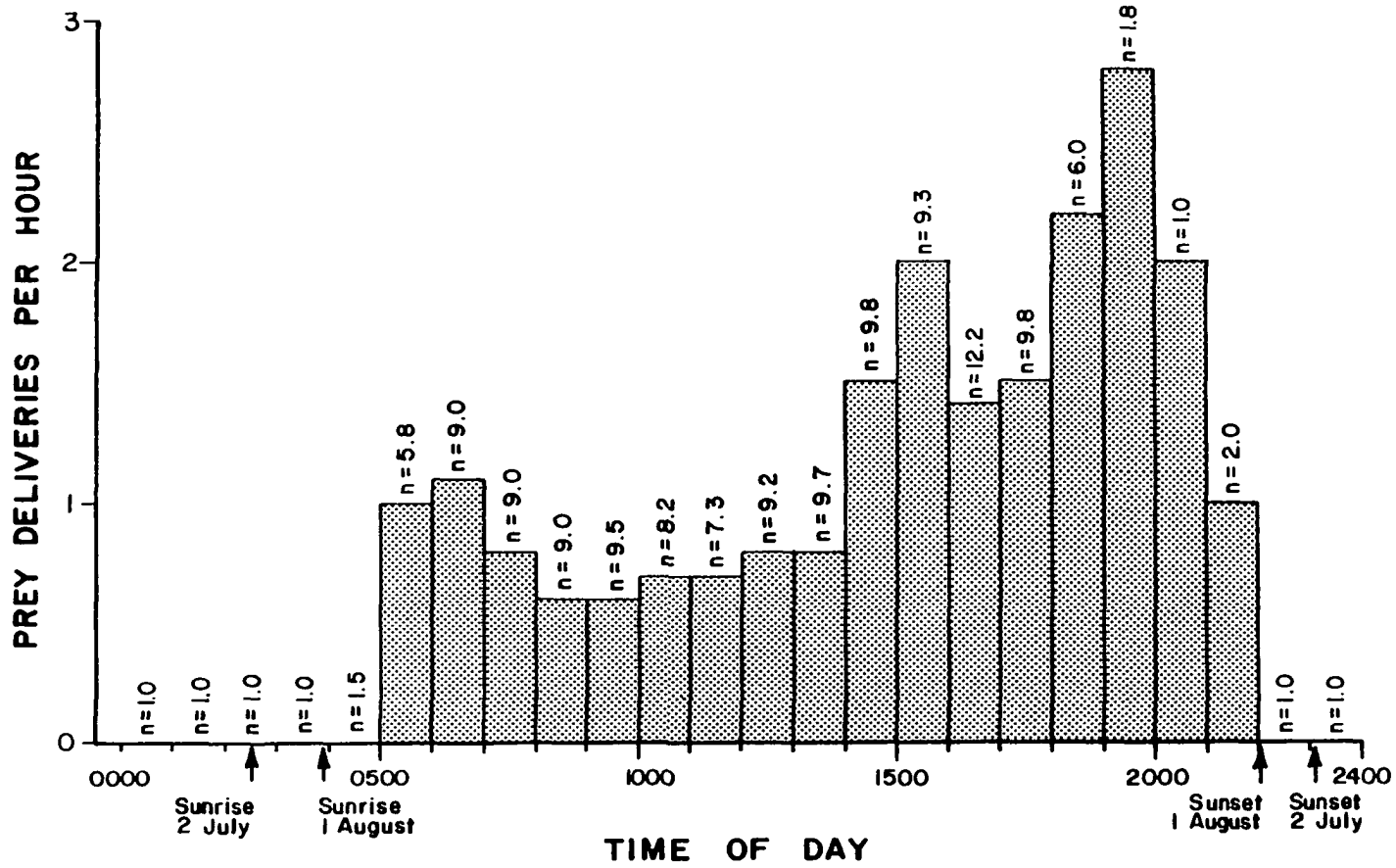
Figure 7.   Delivery of prey by sharp-shinned hawks through the day, Campus 1978 nest, interior Alaska.

Table 17. Prey deliveries by adult sharp-shinned hawks, interior Alaska, Campus 1978 nest.

Weeks After Hatching	Hours of Observation	Total Number of Feedings Observed	Feedings per Hour	Average Prey Weight (See Fig. 14)	Estimated Grams of Prey Delivered per Hour
1	32.2	29	0.90	18.26	16.4
2	25.5	25	0.98	17.04	16.7
3	18.3	19	1.04	17.04	17.7
4	20.8	15	0.72	19.58	14.1
5	21.1	15	0.71	19.58	13.9
6	9.1	6	0.66	19.14	12.6
Total	127.0	109			

clutches of six eggs, two days passed between the pipping of the first egg and the emergence of the last nestling.

Behavior of Young. Young hatched with their eyes open and were covered with a thin coat of white down. Females first fed nestlings by placing tiny bits of heart, liver, or pectoral muscle in their open beaks. Although very young nestlings were too weak and poorly coordinated to take rood from the female's beak, they were able to direct their posteriors toward the nest edge and forcibly eject excreta outward. In 2 or 3 days, nestlings could hold their heads up long enough to snatch food offered by the female. Nestlings regurgitated castings as early as 3 days of age, indicating that they consumed bone and feather fragments at a very early age.

Males developed motor skills and acquired flight plumage more rapidly than females. By 7 or 8 days of age, males exhibited new skills about a day before females and by the end of the nestling period, the gap had widened to about three days. By 7 days of age, when females ceased constant brooding of young, nestlings had a thicker coat of gray down and sheaths of remiges had appeared. By day 8, a buffy down replaced the gray and sheathed retrices began to protrude. At 10 days of age, remiges had begun to burst their sheaths and nestlings began moving to the nest edges and defecating downward instead of horizontally/outward. They began attempts to stand by 13 days, when retrices opened and contour feathers began to appear through the down on the back. The formerly dark brown eyes turned grayish and

breast feathers had appeared by day 14 or 15. By 16 days, nestlings stood for extended periods of time, held prey with their feet while tearing at it with their beaks and began exercising flight muscles by flapping.

Beginning about two weeks after hatching, nestlings mobbed their food-carrying parents, often quite violently. Loose food at nests invariably elicited free-for-alls among nestlings, but as soon as one took decisive control of the prey, the others seemed to lose interest, quieted down and moved away from the bird with the food. I saw no instances of extended squabbling or aggression between nestlings. Food-begging vocalizations were uttered liberally by young whenever parent birds appeared, whether parents carried prey or not. Much squealing and whining accompanied feedings by parents, but when prey was merely left at nests, vocalizations ceased when one nestling took possession of the food.

By 20 days, nestlings appeared more feathered than downy and spent most of their time preening, stretching, scratching and even standing on one leg. They could dissect prey entirely on their own and began moving out onto branches adjoining nests. Young made their first flights by 23-26 days ($\bar{X}$ = 24.4, SD = 1.5, n = 5), with males preceding females by 1 or 2 days.

GROWTH OF YOUNG

Wild Birds. I measured 34 wild nestlings (15 male, 14 female, 5 unsexed) (Table 18). Mean growth in weight, tarsus length and length

Table 18. Measurements of wild sharp-

Age in Days	$\overline{X}$ Weight in g (n, SD)
MALES (15 birds from 8 nests)	
0	11.8 (1, 0.0)
1	19.8 (1, 0.0)
2	22.3 (1, 2.40)
3	22.7 (1, 5.27)
4	-- --
5	41.1 (2, 4.45)
6	35.8 (1, 0.0)
7	51.3 (1, 0.0)
8	-- --
9	73.8 (2, 1.13)
10	82.4 (6, 6.59)
11	81.3 (1, 0.0)
12	87.8 (4, 8.79)
13	96.8 (3, 3.46)
14	-- --
15	104.7 (4, 1.80)
16	106.0 (5, 4.84)
17	114.6 (2, 2.19)
18	116.2 (4, 3.04)
19	111.6 (4, 5.13)
20	114.8 (3, 2.91)
21	-- --
22	115.1 (3, 3.57)
FEMALES (7 birds from 3 nests)	
0	13.2 (2, 0.42)
1	15.8 (6, 3.51)
2	25.9 (1, 0.0)

$\overline{X}$ Tarsus Length in mm (n, SD)	$\overline{X}$ Seventh Primary Length in mm (n, SD)	
	Total Length	Open Portion
-- --	-- --	-- --
-- --	-- --	-- --
-- --	-- --	-- --
-- --	-- --	-- --
-- --	-- --	-- --
29.4 (2, 2.55)	4.7 (2, 1.98)	0.0 (2, 0.0)
26.2 (2, 0.14)	2.4 (1, 0.0)	0.0 (1, 0.0)
36.2 (1, 0.0)	-- --	-- --
-- --	-- --	-- --
40.8 (2, 2.40)	19.5 (2, 5.30)	1.0 (2, 0.42)
42.4 (6, 3.13)	21.4 (2, 9.69)	4.0 (2, 0.0)
44.9 (1, 0.0)	27.0 (1, 0.0)	3.4 (1, 0.0)
44.4 (4, 2.91)	23.3 (1, 0.0)	2.1 (1, 0.0)
47.7 (3, 2.38)	47.3 (1, 0.0)	13.2 (1, 0.0)
-- --	-- --	-- --
49.0 (4, 0.26)	50.2 (1, 0.0)	19.5 (1, 0.0)
49.7 (4, 1.41)	46.0 (1, 0.0)	16.0 (1, 0.0)
51.3 (2, 0.42)	68.0 (1, 0.0)	34.5 (1, 0.0)
51.9 (5, 0.72)	65.6 (1, 0.0)	34.0 (1, 0.0)
49.8 (5, 0.89)	61.9 (1, 0.0)	32.5 (1, 0.0)
50.1 (3, 1.49)	82.6 (1, 0.0)	50.4 (1, 0.0)
-- --	-- --	-- --
52.8 (3, 0.32)	-- --	-- --
-- --	-- --	-- --
-- --	-- --	-- --
-- --	-- --	-- --

Table 18. (continued).

Age in Days	$\overline{X}$ Weight in g (n, SD)	$\overline{X}$ Tarsus Length in mm (n, SD)	$\overline{X}$ Seventh Primary Length in mm (n, SD)	
			Total Length	Open Portion
FEMALES (continued)				
3	-- --	-- --	-- --	-- --
4	30.8 (5, 3.20)	22.3 (2, 1.27)	0.0 (1, 0.0)	0.0 (1, 0.0)
5	55.7 (1, 0.0)	28.9 (1, 0.0)	5.3 (2, 0.07)	0.0 (2, 0.0)
6	-- --	32.6 (1, 0.0)	-- --	-- --
7	57.9 (3, 0.35)	32.0 (5, 1.82)	6.1 (2, 0.28)	0.0 (2, 0.0)
8	71.5 (2,11.31)	34.6 (2, 2.47)	10.3 (2, 4.17)	0.0 (2, 0.0)
9	111.4 (2, 2.40)	43.7 (2, 0.99)	20.5 (2, 0.14)	1.6 (2, 0.85)
10	93.5 (2, 3.61)	41.0 (2, 0.64)	14.9 (1, 0.0)	0.0 (1, 0.0)
11	110.6 (4, 1.00)	43.8 (4, 1.48)	23.0 (3, 0.68)	1.3 (3, 0.60)
12	119.8 (3,17.09)	46.5 (3, 2.99)	34.3 (1, 0.0)	6.0 (1, 0.0)
13	130.1 (6, 9.47)	49.5 (6, 2.03)	38.0 (4, 4.89)	8.0 (4, 3.40)
14	147.7 (1, 0.0)	50.3 (1, 0.0)	37.6 (1, 0.0)	7.8 (1, 0.0)
15	138.0 (2,11.31)	51.1 (2, 0.14)	-- --	-- --
16	154.1 (4, 3.66)	53.8 (4, 0.91)	59.3 (1, 0.0)	23.6 (1, 0.0)
17	166.5 (7,15.18)	55.2 (7, 3.61)	60.8 (5, 6.53)	23.9 (5, 5.90)
18	175.3 (1, 0.0)	59.5 (1, 0.0)	-- --	-- --
19	176.4 (4, 9.11)	56.5 (4, 0.64)	78.0 (1, 0.0)	39.5 (1, 0.0)
20	179.5 (6, 9.75)	56.8 (6, 1.20)	80.4 (4, 4.02)	43.4 (4, 2.80)
21	-- --	-- --	-- --	-- --
22	185.2 (1, 0.0)	60.1 (1, 0.0)	-- --	-- --
23	192.1 (1, 0.0)	56.8 (1, 0.0)	-- --	-- --
UNSEXED (5 birds from one nest)				
0	-- --	-- --	-- --	-- --
1	14.7 (1, 0.0)	-- --	-- --	-- --
2	18.6 (4, 2.45)	-- --	-- --	-- --

-- no data

of the seventh primary are shown in Figures 8, 9 and 10. Growth curves assumed the expected sigmoid form (Ricklefs 1968). Females gained weight and increased in body size faster than males. These complementary growth strategies allow the more active and coordinated males to compete equally for food with their larger sisters (Moss 1979).

Captive-reared Birds. The captive-reared young grew faster and attained greater size than the wild young (Table 19, Figures 8, 9 and 10), which contrasts with Tinbergen's (1946) hypothesis that accipiters "overfeed" their young. A larger sample size might establish confidence intervals that would show no significant difference between wild and captive young, but my limited data suggest that none of the wild nestlings fulfilled their potential for growth.

Young sharp-shinned hawks fledge 23-26 days after hatching, faster than any other North American raptor, implying not only a small body size and short nest time needed to attain size, but also rapid growth and efficient conversion of food to body tissue. At their peak, the hand-reared young assimilated about half of the food they ate (Figure 11). Assuming only about 70 percent of food is metabolically available (Reynolds 1978), this rate of assimilation would seem remarkable, but it is similar to that found in other raptors (Olendorff 1974). Because feces were insubstantial and castings were small, I suspect that much more than 70% of the food supplied was metabolically available, but actual caloric measurements of food and waste were not made.

The hand-reared male consumed approximately 490 g of food in at-
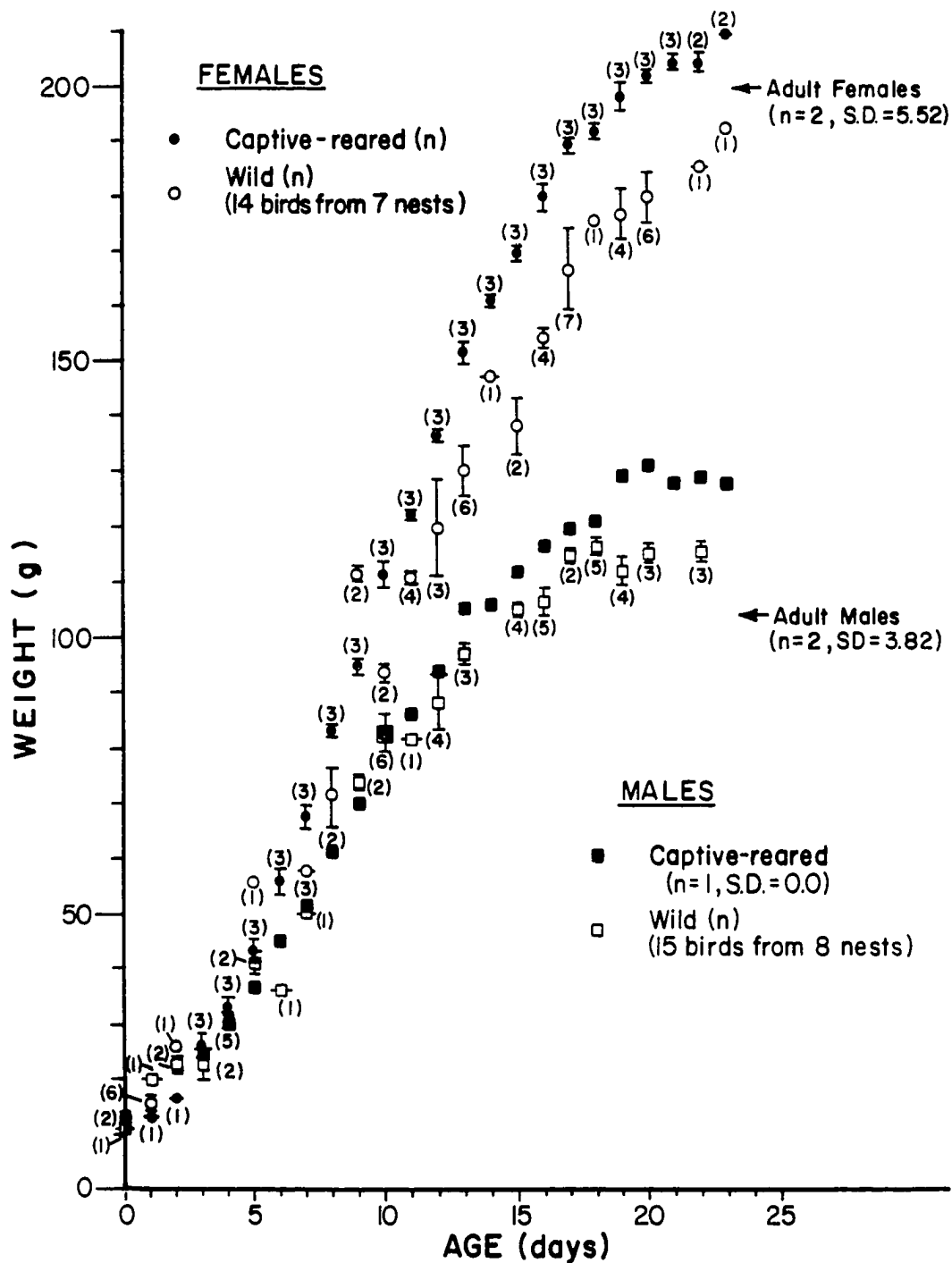
Figure 8. Mean weight gain of nestling sharp-shinned hawks, interior Alaska, 1979 and 1980. Vertical lines indicate one standard deviation.
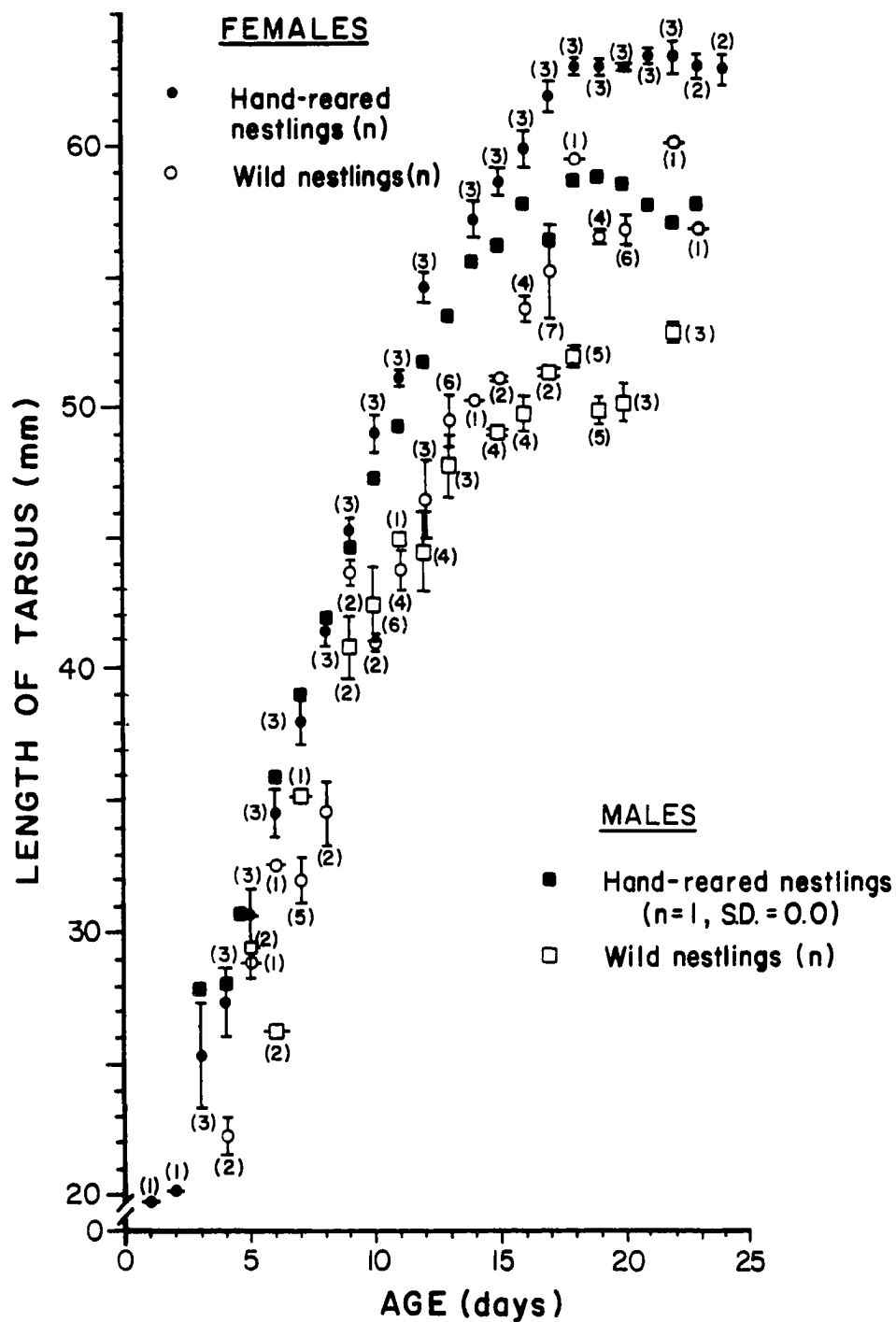
Figure 9. Mean growth of tarsus of nestling sharp-shinned hawks, interior Alaska, 1979 and 1980. Vertical lines indicate one standard deviation.
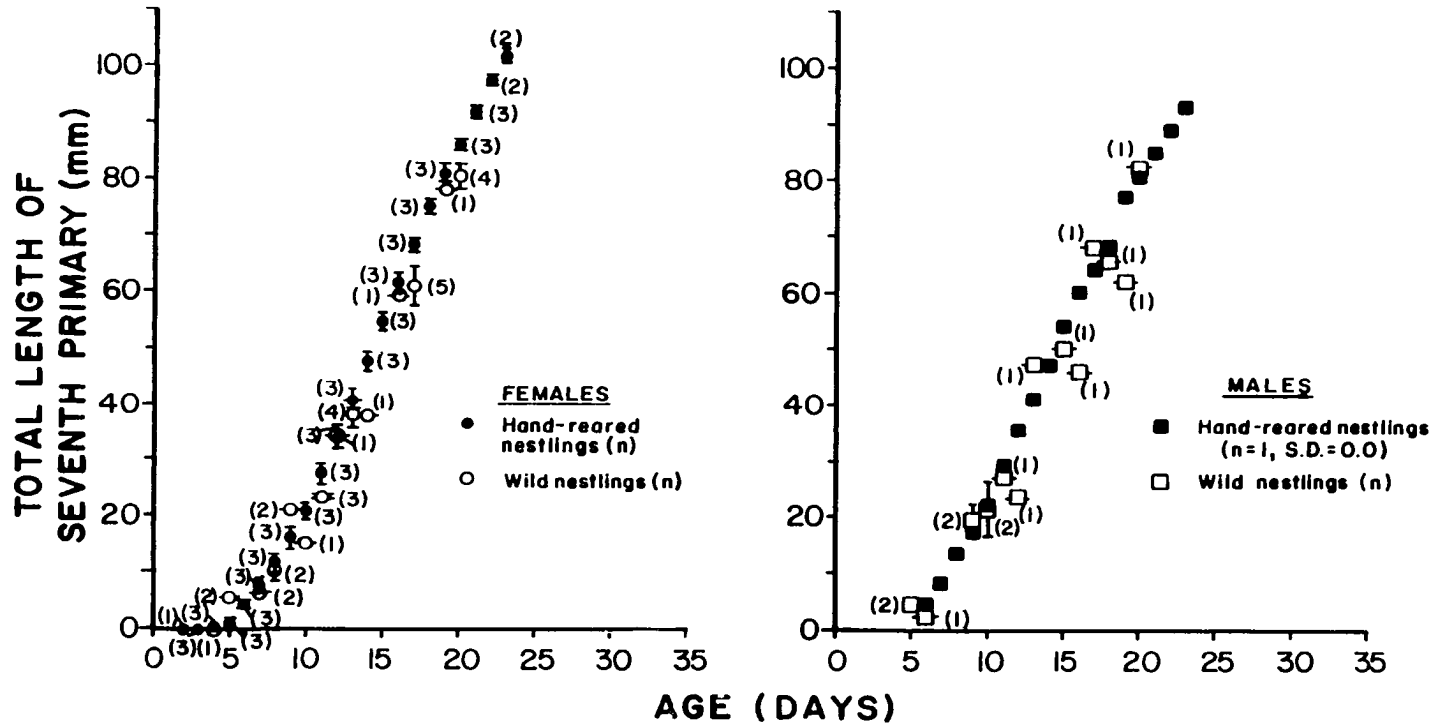
Figure 10. Mean growth of seventh primary of nestling sharp-shinned hawks, interior Alaska, 1979 and 1980. Vertical lines indicate one standard deviation.

Table 19. Measurements of captive-reared sharp-shinned hawks, interior Alaska, 1979.

			$\bar{X}$ Seventh Primary Length in mm	
Age in Days	$\bar{X}$ Weight in g	$\bar{X}$ Tarsus Length in mm	Total Length	Open Portion
MALES (n=1, SD=0.0)				
0	--	--	--	--
1	--	--	--	--
2	--	--	--	--
3	24.6	27.8	--	--
4	29.9	28.0	--	--
5	36.5	30.7	--	--
6	45.1	35.8	4.7	0.0
7	51.4	38.9	8.4	0.0
8	61.2	41.8	13.5	0.0
9	70.0	44.6	17.5	0.0
10	82.3	47.2	22.2	1.5
11	85.8	49.2	29.1	3.1
12	93.5	51.6	35.4	6.2
13	104.9	53.4	41.2	13.0
14	105.6	55.5	47.1	16.1
15	111.6	56.1	54.0	20.3
16	116.0	57.7	60.3	25.5
17	119.2	56.3	64.2	32.0
18	120.6	58.6	68.4	40.1
19	128.9	58.7	77.1	50.3
20	130.8	58.4	81.0	49.8
21	127.2	57.6	85.0	55.9
22	128.3	56.9	89.1	83.8
23	127.5	57.7	93.1	88.0

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Table 19. (continued).

| Age in Days	$\overline{X}$ Weight in g (n, SD)	$\overline{X}$ Tarsus Length in mm (n, SD)	$\overline{X}$ Seventh Primary Length in mm (n, SD)	
			Total Length	Open Portion
FEMALES				
0	-- --	-- --	-- --	-- --
1	13.5 (1, 0.0)	19.8 (1, 0.0)		
2	16.8 (1, 0.0)	20.2 (1, 0.0)	0.0 (1, 0.0)	0.0 (1, 0.0)
3	26.2 (3, 4.22)	25.4 (3, 3.95)	0.0 (3, 0.0)	0.0 (3, 0.0)
4	33.0 (3, 3.45)	27.4 (3, 2.27)	0.3 (3, 0.49)	0.0 (3, 0.0)
5	43.2 (3, 4.01)	30.7 (3, 2.01)	0.7 (3, 1.27)	0.0 (3, 0.0)
6	55.9 (3, 4.47)	34.6 (3, 1.68)	4.4 (3, 0.87)	0.0 (3, 0.0)
7	67.5 (3, 4.05)	38.1 (3, 1.78)	7.3 (3, 1.86)	0.0 (3, 0.0)
8	83.0 (3, 2.31)	41.5 (3, 1.27)	11.6 (3, 2.98)	0.0 (3, 0.0)
9	94.7 (3, 3.27)	45.3 (3, 1.08)	15.8 (3, 3.42)	0.0 (3, 0.0)
10	111.1 (3, 4.42)	49.0 (3, 1.53)	20.5 (3, 2.80)	0.8 (3, 1.36)
11	122.0 (3, 1.31)	51.1 (3, 0.75)	27.5 (3, 3.46)	2.4 (3, 1.13)
12	136.3 (3, 2.17)	54.6 (3, 0.97)	33.9 (3, 4.11)	4.8 (3, 3.29)
13	151.3 (3, 3.84)	57.2 (3, 1.38)	40.8 (3, 3.23)	6.1 (3, 4.64)
14	160.6 (3, 1.29)	58.7 (3, 1.01)	47.6 (3, 3.27)	13.2 (3, 3.16)
15	169.4 (3, 3.61)	59.9 (3, 1.36)	54.7 (3, 3.38)	18.9 (3, 3.80)
16	179.4 (3, 5.20)	61.9 (3, 1.23)	61.4 (3, 2.89)	23.7 (3, 1.85)
17	189.0 (3, 2.87)	63.0 (3, 0.64)	68.2 (3, 2.04)	32.1 (3, 1.60)
18	191.4 (3, 2.50)	63.0 (3, 0.59)	75.0 (3, 2.34)	37.7 (3, 3.66)
19	197.8 (3, 5.14)	63.0 (3, 0.26)	80.8 (3, 2.55)	45.4 (3, 4.88)
20	201.5 (3, 2.15)	63.4 (3, 0.65)	86.0 (3, 1.97)	54.7 (3, 2.22)
21	204.0 (3, 2.45)	63.4 (3, 1.12)	91.5 (3, 2.16)	58.4 (3, 2.91)
22	203.8 (2, 3.61)	63.0 (2, 1.06)	97.4 (2, 1.84)	69.4 (2, 1.34)
23	209.3 (2, 0.07)	62.9 (2, 1.27)	101.8 (2, 2.19)	73.5 (2, 3.18)

-- no data

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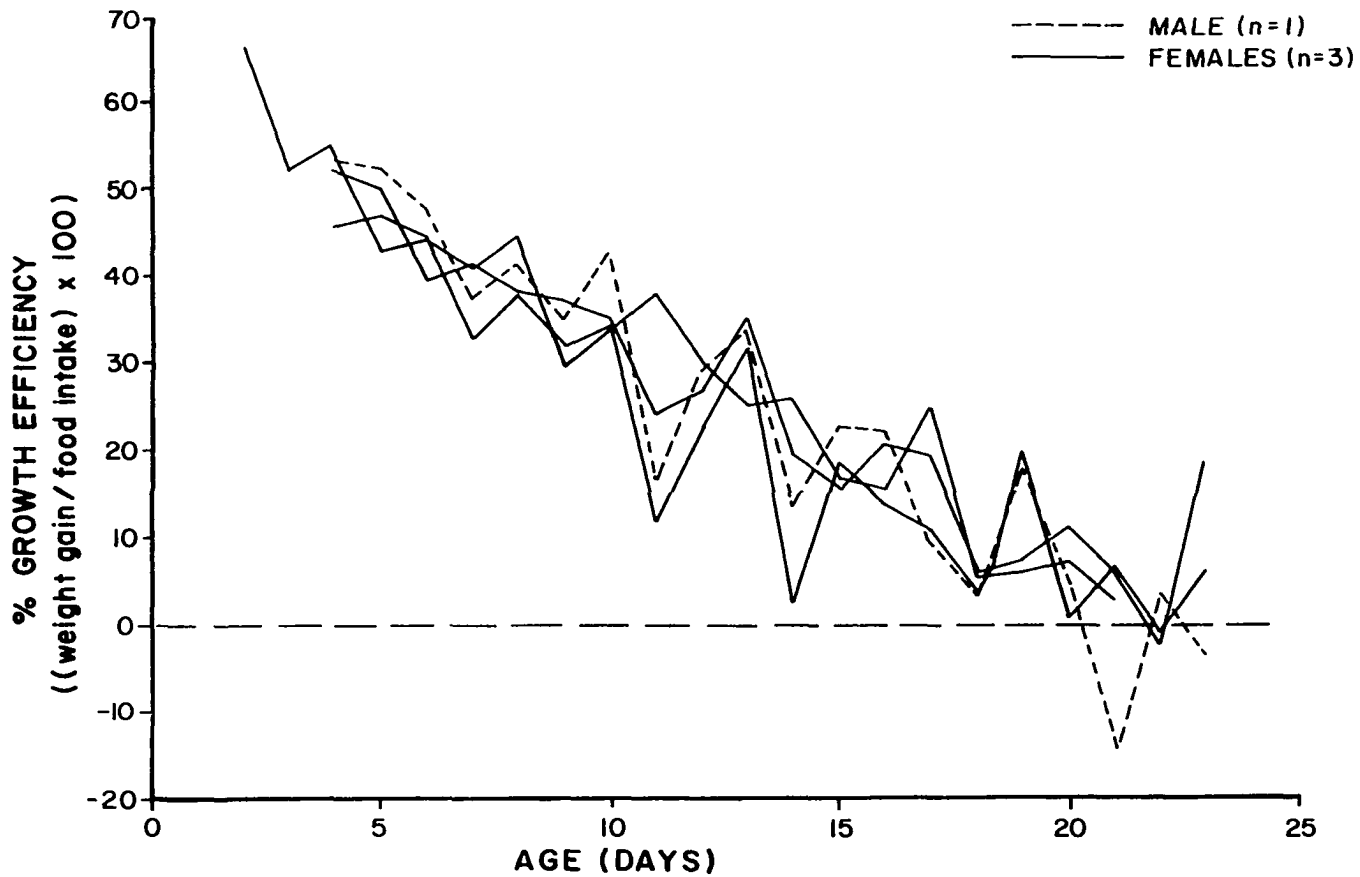
Figure 11. Percentage of food consumed (g) which was converted to body weight (g) in four captive-reared sharp-shinned hawks, interior Alaska, 1979.

taining a maximum weight of 130.8 g, indicating an overall growth efficiency of 26.7%. Females ate an average of 870 g and reached an average maximum weight of 207.1 g, indicating a growth efficiency of 23.8%. Sharp-shinned hawks required less food per gram of hawk produced than did other raptors studied (Table 20). This is in marked contrast to Olendorff's (1974) assumption that smaller hawks are less efficient in conversion of food to tissue, because of relatively greater heat loss from small bodies. The difference between these sharp-shins and Olendorff's (1974) buteos is probably due to richer food supplied over a shorter growth period rather than a more efficient conversion of food to tissue in sharp-shinned hawks.

FLEDGING AND POST-FLEDGING PERIOD

Young sharp-shinned hawks fledged as early as 16 July and as late as 30 July ($\overline{X}$ = 21, SD = 4.1, n = 8).

Behavior of Adults. Parent birds were not often seen during the fledgling period. Females ceased perching near nests about the time fledglings began venturing into nearby trees. They may have been hunting, as 1) they were often absent from nest sites for as long as two hours and 2) they sometimes delivered prey to the nests with no apparent involvement by their mates, i.e., no food-transfer vocalizations were heard. Conversely, they may have been perching out of sight of the nest, as Zachel (pers. comm.) observed frequently in his study of interior Alaskan goshawks.

Females deposited prey at nests and left immediately. When

Table 20. Growth efficiency of captive-reared raptors.

Source	Species	Grams Eaten per Gram of Raptor Produced	Total Days
This Study	sharp-shinned hawk male	3.75	23
	female	4.2	23
Olendorff 1974	ferruginous hawk (_Buteo regalis_)	4.7	45
	red-tailed hawk (_Buteo jamaicensis_)	4.7	45
	Swainson's hawk (_Buteo swainsoni_)	5.7	45

fledglings could fly proficiently, females often hurled prey at nests and retreated. Rumors of hawks releasing live prey for fledglings to catch may have their roots in observations of similar behaviors, i.e., tossed dead prey was mistaken for live. I saw neither deliveries of live prey (Meng 1959) nor use of artificial "lures" (Ravel 1981) to entice rledglings to fly. During the post-fledging period, males appeared only long enough to transfer food to females.

Behavior of Young. First flights were short, but surprisingly strong and sure. Nestlings tirst ventured to nearby trees and returned in a rew minutes, and by 5 or 6 days post-fledging, young hawks strayed up to 50 m from nests for as long as an hour. I observed no instances of rledglings missing intended perches or landing on unstable perches and hanging upside down, as is commonly seen in raptors. However, in 1980, I found a recently-fledged female dead on the ground 15 m from the Banner Creek nest; post mortem examination revealed that the bird died of blunt trauma, possibly associated with a collision with an intended perch, suggesting that not all fledglings are as expert at flight as those I observed.

Delivery of prey to the nest elicited food-begging calls from nearby young which alerted wide-ranging fledglings, and young hawks quickly converged on the nest, vocalizing constantly. As before, competition and vocalization ceased when one bird took control of the prey. Beginning at about 5 days post-fledging, young hawks carried prey from the nest to the ground to eat. Siblings followed a prey-

carrying bird to the ground, but abandoned the chase when it reached the ground and mantled over the prey.

Fledglings spent much of their time sunning, preening and stretching, with occasional forays into nearby trees. I noted five separate instances of young birds bathing in puddles on a gravel road near the Campus 1978 site. Fledglings frequently chased one another, parent birds and nearly anything that moved within their sight. Many chases appeared to be pursuit of potential prey, but only one instance could be confirmed: on 6 August 1978, just 16 days after fledging, a male flew nearly vertically from the ground to above the forest canopy, a distance of about 20 m, captured an unidentified sparrow, returned to the ground and ate it. I saw fledglings apparently chasing prey when they were only 30 days old -- ten days earlier than sharp-shinned hawks observed by Mueller et al. (1981).

PRODUCTIVITY

Clutch Size. Mean clutch size for the study period was 5.1 (Table 21). Two eggs disappeared in mid-incubation from the Dogpatch 1979 nest. The agent of or agents responsible for the removal of these eggs were not identified. A third egg was collected from the same nest after it was discovered to be punctured.

Hatching success. Thirty-four of 41 eggs (82.9%) hatched (Table 22). The mean number of nestlings per nest was 4.4 (Table 21). Except for the three eggs discussed above, there were no apparent reasons why eggs did not hatch. One egg from the Chena 1979 nest seemed to be

Table 21. Mean number of eggs laid, eggs hatched and young fledged per nest for sharp-shinned hawks in interior Alaska, 1978-1981.

Year	Mean Number of Eggs (n, SD)	Mean Number of Eggs Hatched (n, SD)	Mean Number of Young Fledged per Nest Attempt (n, SD)
1978	---	5.0 (2, 0.0)	5.0 (2, 0.0)
1979	5.0 (3, 1.0)	4.2 (5, 1.92)	2.8 (5, 1.64)
1980	5.3 (4, 0.5)	4.3 (4, 1.5)	2.5 (4, 2.08)
1981	5.0 (1, 0.0)	4.3 (3, 1.53)	1.7 (3, 1.53)
Total	5.1 (8, 0.64)	4.4 (14, 1.40)	3.1 (14, 1.86)

infertile, or at least the embryo died very early in its development. One egg from the Backyard 1979 nest and two from Chena 1980 had well-developed embryos within them, but they died before hatching.

Fledging Success. Twenty-seven of 34 (79.4%) eggs that hatched produced young that fledged (Table 22). At least 43 of 62 (69.4%) nestlings fledged. The mean number of nestlings that fledged was 3.1 per nest (Table 21). Six nestlings were taken from nests for growth study, four from the Banner Creek 1979 nest and two from the Moose Creek 1980 nest. One nestling from the Dogpatch 1980 nest died while being measured. Twelve nestlings disappeared from nests. All four nestlings from the Springer 1981 nest and the remaining two from the Moose Creek 1980 nest vanished, leaving only a few partially-grown flight feathers behind. The fact that these feathers appeared to have been forcibly pulled from the nestlings may implicate goshawks in the disappearance and assumed death of the sharp-shins. One young bird at the Banner Creek 1981 nest and three at Melchior 1981 disappeared without a trace. One recently-fledged sharp-shin was found dead near the Banner 1980 nest, apparently, as discussed earlier, a victim of its own lack of flying experience (Krasch and Berne 1980).

Of 12 deaths or disappearances not apparently related to my actions, 8 (66.7%) occurred in 1981, a year of cooler temperatures and greater rainfall than normal (unpubl. data, National Weather Service, Fairbanks). Perhaps parent birds had difficulty hunting in wet foliage and were unable to satisfy the nutritional needs of the young, which

Table 22. Hatching and fledging success of sharp-shinned hawks in interior Alaska, 1979-1981.

Year	Number of Nests	Eggs Hatched/ Eggs Laid (%)	Young Fledged/ Eggs Hatched (%)
1979	3	10/15 (66.7)	10/10 (100) (n = 2)
1980	4	18/20 (90)	14/18 (77.8)
1981	1	6/6 (100)	3/6 (50)
TOTAL	8	34/41 (82.9)	27/34 (79.4)

led to starvation or cannibalism.

Productivity. Sharp-shinned hawks in Alaska laid more eggs and hatched more young per nest than those studied elsewhere (Table 14). Mean number of young fledged per nest was greater than or comparable to values observed elsewhere (Table 14). These figures may reflect more favorable nesting conditions in Alaska, as speculated earlier.

Mortality. Because of the secretive and highly mobile nature of these birds, post-fledging mortality will probably be the last aspect of sharp-shinned hawk ecology to be completely and accurately described. Newton (1979) reported that in known studies, first-year mortality of raptors ranged from 50% to 83%. First-year mortality of accipiters was greater than that for other genera (Table 23). Rates of mortality of adults are less well-known, but are generally considerably less than those for young birds. I suspect the same applies to sharp-shinned hawks in Alaska, but during the study period, I encountered only three dead sharp-shinned hawks in addition to those immatures mentioned earlier. All were adults killed by striking windows, and were brought to me by other investigators.

DISPERSAL AND FALL MIGRATION

Dispersal. Twenty to twenty-five days post-fledging, the Campus 1978 family unit apparently split up. Often, several hours of observation in the blind passed with no evidence of the presence of hawks. Food deliveries were infrequent and made to individual fledglings rather than to the nest. A family of sharp-shinned hawks in Utah dis-

Table 23. Rates of first-year mortality in some accipiter hawks.[1]

Species	% Mortality in First Year	Source
European sparrowhawk	62	Kramer 1973
(Accipiter nisus)	68	Tinbergen 1946
	63	Schelde 1960
	70	Newton 1975
Cooper's hawk	83	Henny and Wight 1972
(Accipiter cooperii)	78	Henny and Wight 1972
goshawk	63	Haukioja and Haukioja 1970
(Accipiter gentilis)	58	Kramer 1973
	64	Saurola 1976

[1]After Newton (1979)

banded at a similar point in the development of the fledglings (Platt 1973).

By the seventh week after hatching, Mueller et al. (1981) observed 1) a "drastic" decrease in the amount of prey delivered to young sharp-shins, 2) a noticeable influx of migrant passerines and 3) a rapid increase in "predatory episodes" by fledglings. In this study, prey deliveries to the nest decreased late in the fledgling period (Table 16 and Figure 12), although birds had scattered by the seventh week and close observation was not possible. I saw fledglings apparently chasing prey when there were many immature passerines about, well before migrant passerines appeared.

Captive-reared birds, despite having human surrogate parents, showed similar patterns of learning and dispersal. Apparently, sharp-shinned hawk fledglings are able to care for themselves, depending on the adults only for food. The process of learning to pursue and capture prey depends more on the number of opportunities to chase potential prey rather than on "instruction" from parent birds.

Fall Migration. Shortly after the apparent breakup of family units, usually in late August, large numbers of songbirds began passing through, and sharp-shinned hawks probably followed them along in the southward migration. Most sharp-shins had left the Fairbanks area by early September, although there are isolated records of individuals in the area practically year-round (Kessel 1967 and unpubl. data 1952-1982).
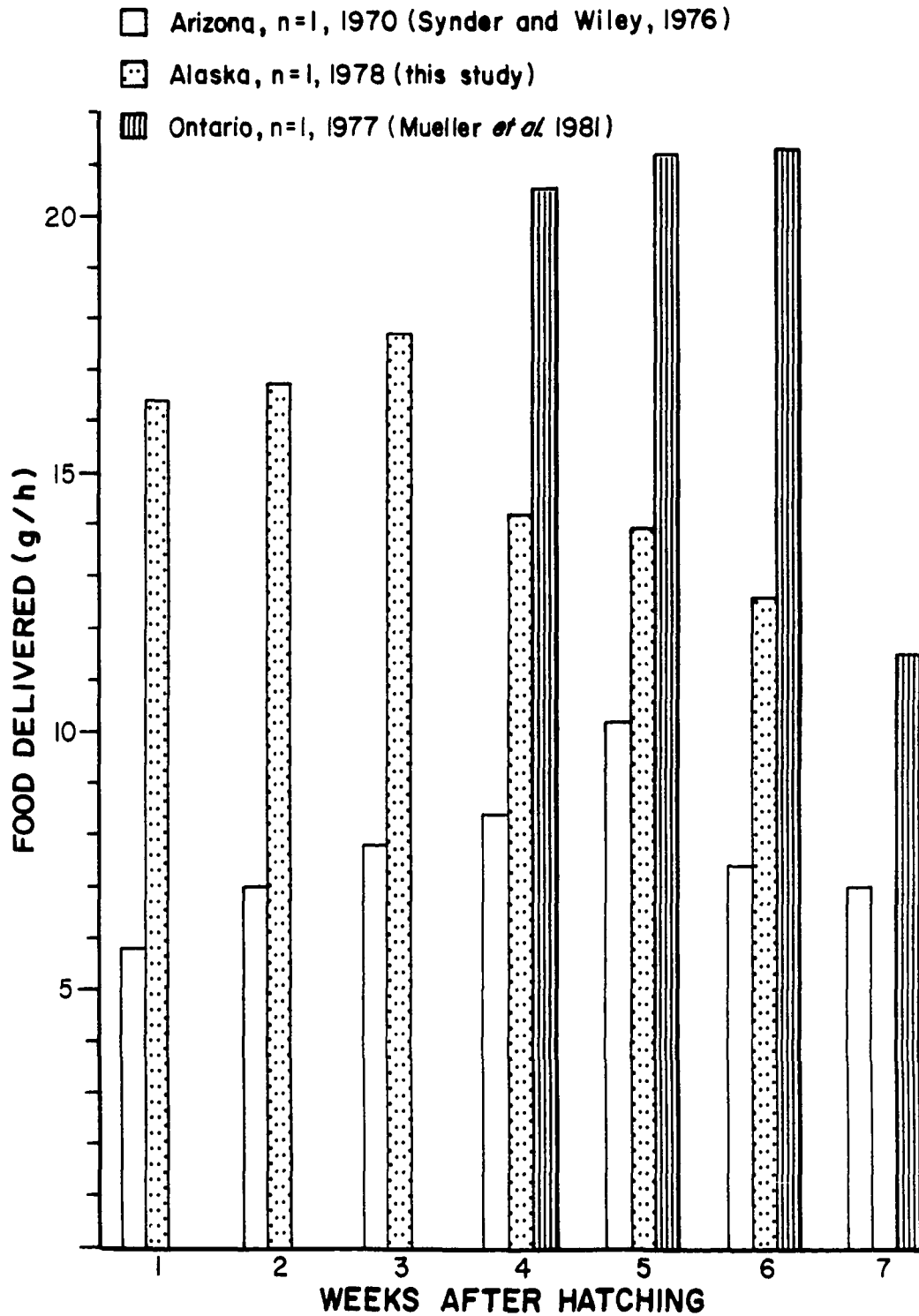
Figure 12. Rates of prey delivery by sharp-shinned hawks through the breeding season.

II. FEEDING ECOLOGY

Remains from 14 nest sites represented 1159 individual prey items of at least 42 species (Table 24). Nearly 83% of the prey items (937 birds, 24 mammals) were assigned to seven half-month periods during the summer, the rest coming from infrequently-visited sites where accurate designation was not possible.

I examined 267 castings. Identification of prey animals from castings was frequently impossible, as feathers and hair were mutilated or semi-digested. Presence or absence of several basic types of prey fragments was determined (Table 16).

I assume that the frequency of occurrence of prey remains is an accurate reflection of the actual diet of the hawks. All <u>Catharus</u> thrush figures are pooled, as they are similar in size and behavior and were often indistinguishable in prey remains.

DIET

Sharp-shinned hawks in this study depended heavily upon small birds (96.9% of diet by biomass), a conclusion reached by other investigators (e.g., Fisher 1893, Bent 1937, Craighead and Craighead 1956, Storer 1966, Snyder and Wiley 1976, Reynolds 1978, Duncan 1980). A strong correlation ($r_s = 0.9061$, $p<0.0005$) exists between frequency of occurrence in diet and importance in diet in terms of biomass, i.e., those prey species taken most frequently contributed heavily to the total biomass of prey. Of the ten species taken most frequently, seven were among the ten greatest contributors to total biomass; 71.05% of

Table 24. Prey remains found at fourteen sharp-shinned hawk nest
sites, interior Alaska, 1979-1981.

Species	Number	% of Total by Number	Biomass (g)	% of Total by Biomass
all Catharus thrushes[1]	192	16.57	5222.1	24.28
dark-eyed junco	155	13.38	2673.8	12.43
American robin	20	1.73	1760.0	8.18
yellow-rumped warbler	106	9.16	1241.2	5.77
white-crowned sparrow	50	4.13	1140.0	5.30
yellow warbler	105	9.06	948.0	4.41
bank swallow	49	4.23	847.7	3.94
fox sparrow	25	2.16	787.0	3.66
varied thrush	10	0.86	785.0	3.65
unidentified (Class 1, 2, 3 or 4)	46	3.97	472.5	2.20
Hammond's flycatcher	39	3.37	423.5	1.97
orange-crowned warbler	41	3.54	379.7	1.76
black-capped chickadee	32	2.77	368.6	1.71
unidentified (Class 2 or 3)	40	3.46	356.3	1.66
savannah sparrow	19	1.65	333.0	1.54
Lapland longspur	12	1.04	327.6	1.52
alder flycatcher	26	2.24	315.0	1.47
redpoll	22	1.91	303.2	1.41
American tree sparrow	16	1.39	277.5	1.28
unidentified (Class 3)	13	1.12	219.8	1.02
northern waterthrush	11	0.95	190.3	0.88
ruby-crowned kinglet	22	1.90	154.0	0.72
Bohemian waxwing	3	0.26	148.3	0.69
Lincoln's sparrow	9	0.78	142.2	0.66
unidentified (Class 2)	15	1.30	127.5	0.60
blackpoll warbler	10	0.87	117.8	0.55
western wood-pewee	8	0.69	108.0	0.50
solitary sandpiper	2	0.17	103.0	0.48
lesser yellowlegs	1	0.09	80.5	0.37
rusty blackbird	2	0.17	73.4	0.34
tree swallow	4	0.35	72.0	0.33
boreal chickadee	6	0.52	63.3	0.30
Townsend's warbler	5	0.43	42.3	0.20
cliff swallow	2	0.17	36.6	0.18
unidentified (Class 4 or 5)	1	0.09	37.9	0.18
spotted sandpiper	1	0.09	37.3	0.17
olive-sided flycatcher	1	0.09	34.1	0.16

Table 24. (continued)

Species	Number	% of Total by Number	Biomass (g)	% of Total by Biomass
unidentified (Class 1 or 2)	4	0.35	30.0	0.14
downy woodpecker	1	0.09	25.8	0.12
Wilson's warbler	2	0.17	15.4	0.08
pine siskin	1	0.09	12.2	0.06
unidentified (Class 1)	1	0.09	7.4	0.03
Total Birds	1130	97.63	20841.6	96.90
northern red-backed vole	17	1.47	450.5	2.09
snowshoe hare	2	0.17	90.0	0.42
unidentified mammals	5	0.43	64.5	0.30
meadow jumping mouse	2	0.17	36.0	0.17
meadow vole or tundra vole	1	0.09	31.0	0.14
shrew	2	0.17	7.0	0.03
Total Mammals	29	2.50	679.0	3.15
TOTAL	1159	100.13	21520.6	100.05

[1] 67 Swainson's or gray-cheeked thrushes, 3 hermit thrushes, 122 Catharus thrushes.

the total number comprised 58.33% of the total biomass (Table 24).

Sharp-shinned hawks showed a marked response to the increased availability of younger age classes of prey animals as the breeding season progressed (Figure 13). Immature prey were very important in the diet, comprising more than 34% of the total biomass (Figure 13); in early July, they constituted a greater proportion of the total avian biomass than did adults. Juveniles were less important, comprising about 6% of avian biomass, and nestlings constituted a negligible amount, 0.58% (Figure 13). The decline in frequency of occurrence of immatures in the prey remains at the end of the breeding season (Figure 13) may be due to the fact that, in many samples, older immatures may be indistinguishable from adults. It is possible, but I think unlikely, that hawks were depleting the numbers of immatures so severely that they depended more heavily on adults late in the season.

Many authors (e.g., Storer 1966, Reynolds 1978, Newton 1979, Geer 1982, Newton and Marquiss 1982a) have emphasized the importance of raptors' timing of the nesting effort so as to coincide with the appearance of young, vulnerable prey. In this study, adult prey were the most important food source, considering the breeding season as a whole. I suspect that because favorable nesting conditions exist only briefly in Alaska, sharp-shinned hawks begin the nesting effort as soon as they arrive on the breeding grounds. A sharp-shinned hawk's ability to anticipate a surge of young prey animals is probably not as important as the capacity to gauge the abundance of adult prey, which must sustain
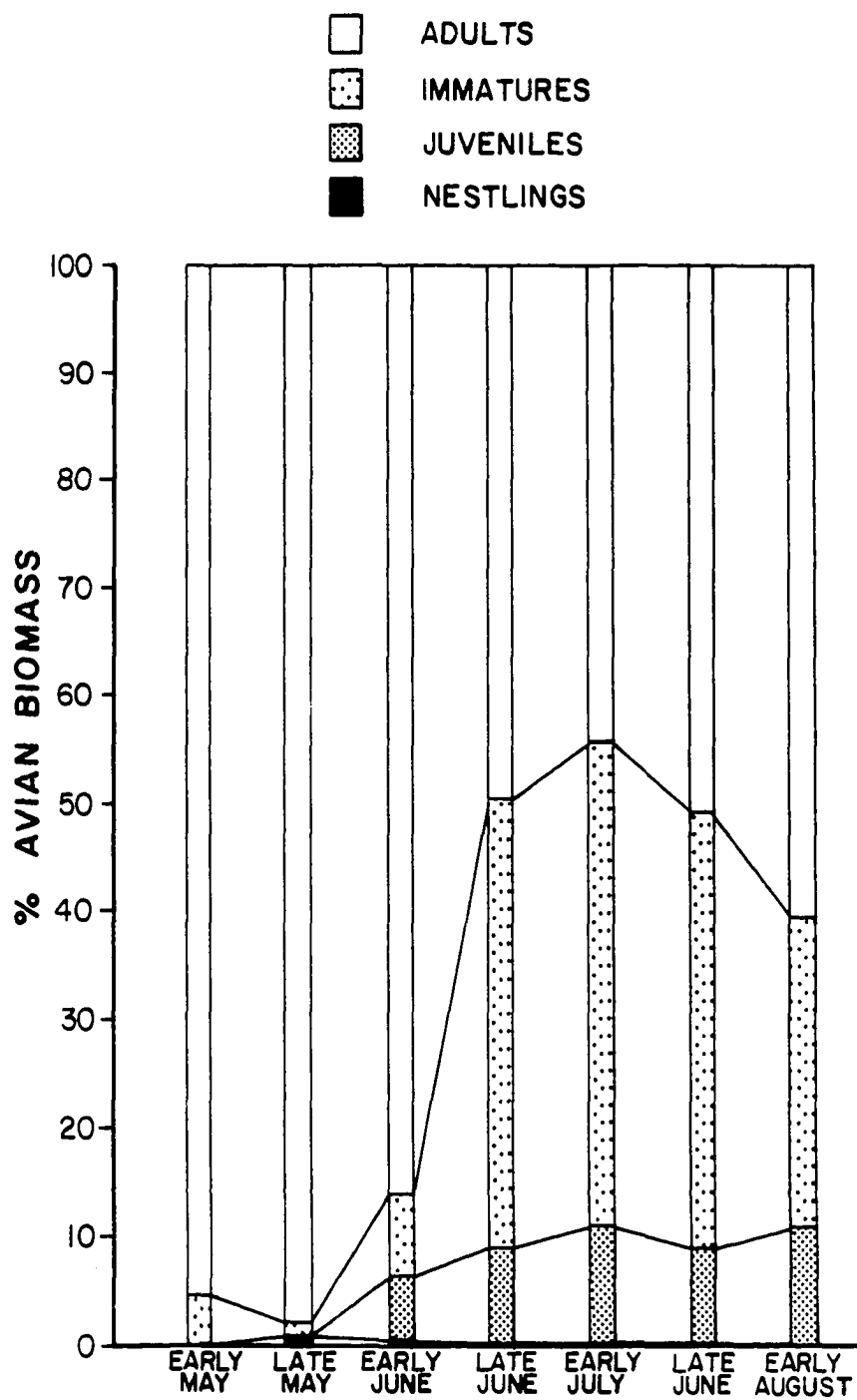
Figure 13. Age class composition of avian prey of sharp-shinned hawks through the breeding season, interior Alaska, 1978-1981.

both parents and offspring until the appearance of many young prey.

Sharp-shinned hawks apparently capture adult and subadult birds proportionally, according to their availability. Breeding and non-breeding adult prey are present throughout the breeding season, and birds of the year remain in the immature stage longer than they do in the nestling and juvenile stages. Thus, the more mobile, presumably more conspicuous older birds are available as prey for a longer period of time than the two younger, more numerous age classes. Older birds appear more frequently and are more important in the diet. Adults and immatures together accounted for more than 93% of the total biomass (Table 25). Younger age classes, especially nestlings, occur infrequently in the prey remains perhaps because the hawks consumed the entire carcasses. Young birds would probably be nearly completely digested and would not be well-represented in regurgitated castings (Errington 1930 and 1932, Newton and Marquiss 1982a). Sharp-shinned hawks certainly eat nestling and juvenile birds (Bent 1937). J. R. Rose (pers. comm.) saw a male sharp-shin attack a brood of yellow-rumped warblers still in their nest, and I have found remains of very young prey birds at plucking perches. I observed several instances of males bringing four to six very small prey items to nests in rapid succession, suggesting that nests of prey birds had been located and the hawks were taking everything in them.

Separating prey into size classes again reveals a pattern of use proportional to availability (Table 26). Comparing avian prey

Table 25. Age class composition of remains of avian prey ot sharp-shinned hawks, interior Alaska, 1978-1981.

Age Class	% of Total by Number	% of Total by Biomass
Adult	51.68	58.72
Immature	33.63	34.72
Juvenile	12.39	5.99
Nestling	2.30	0.58
	100.00	100.01
	(n=1130)	(n=17937.2 g)

Table 26. Size class composition of sharp-shinned nawk prey,
interior Alaska, 1978-1981.

Size Class[1]	% of Total by Number	% of Total by Biomass	Avian Prey Availability[2]
1	10.9b	3.62	1.2
2	38.40	23.49	17.1
3	28.21	29.42	32.6
4	19.15	29.64	18.3
5	0.60	1.68	5.2
6	2.67	12.20	25.6
	99.99 (n=1159)	100.05 (n=18551.7 g)	100.0 (n=122.3)

[1]According to Storer (1966; see Table 2)

[2]Relative abundance of those species listed in Table 4 known to be
taken as sharp-shinned nawk prey (adults only)

availability figures with percentages of total biomass represented by various size classes is difficult; these figures are presented merely to demonstrate that there are no large discrepancies between use of prey and prey availability, according to prey size.

Average prey item weight decreased as the breeding season progressed, perhaps due to the increased incidence of younger prey in the diet (Figure 14). The slight increase in average prey item weight at the end of the season may be a reflection of increased hunting by females (Perrins and Geer 1980, Geer 1981, Newton and Marquiss 1982a). I observed females doing little or no hunting until the late fledgling period (see "Post-fledging Period"). Many authors (e.g., Tinbergen 1946, Höglund 1964, Storer 1966, Reynolds 1972, Snyder and Wiley 1976, Reynolds 1978, Newton 1978, 1979, Kennedy 1980, Geer 1981, Newton and Marquiss 1982a) have suggested that female raptors capture heavier prey than do their smaller male counterparts. However, since there was no apparent significant increase in the rate of capture of heavier prey items at the end of the breeding season (Figure 15), the increase in average prey item weight might be due to young prey animals approaching their adult sizes. If so, an increase in average prey item weight would be evident whether the females hunted or not. I suspect a combination of these two possible explanations produced the increase.

Sharp-shinned hawks frequently ingest insects (Table 16). Some are probably consumed incidentally with the stomachs and gizzards of avian prey, but I suspect that they also intentionally capture and eat
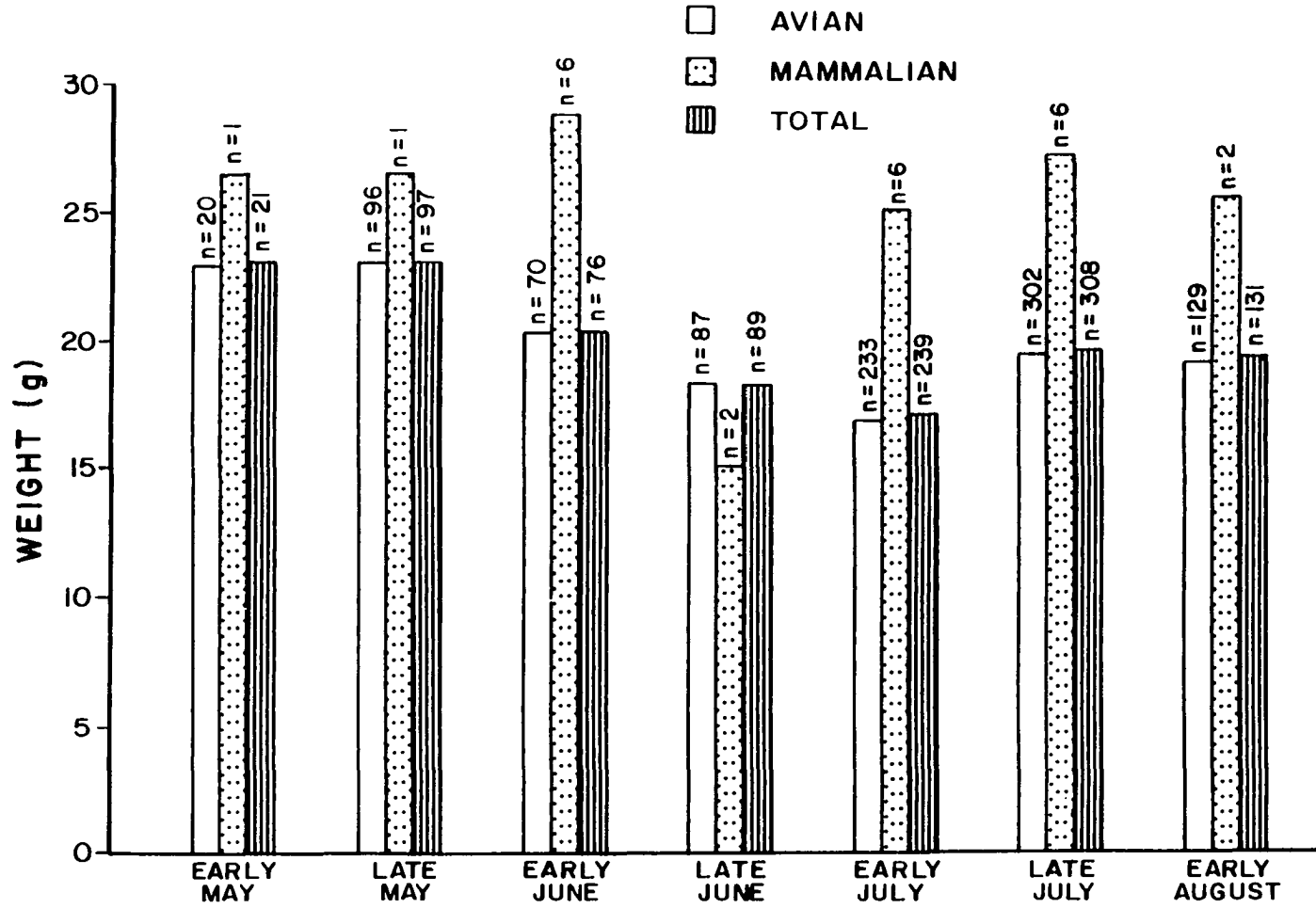
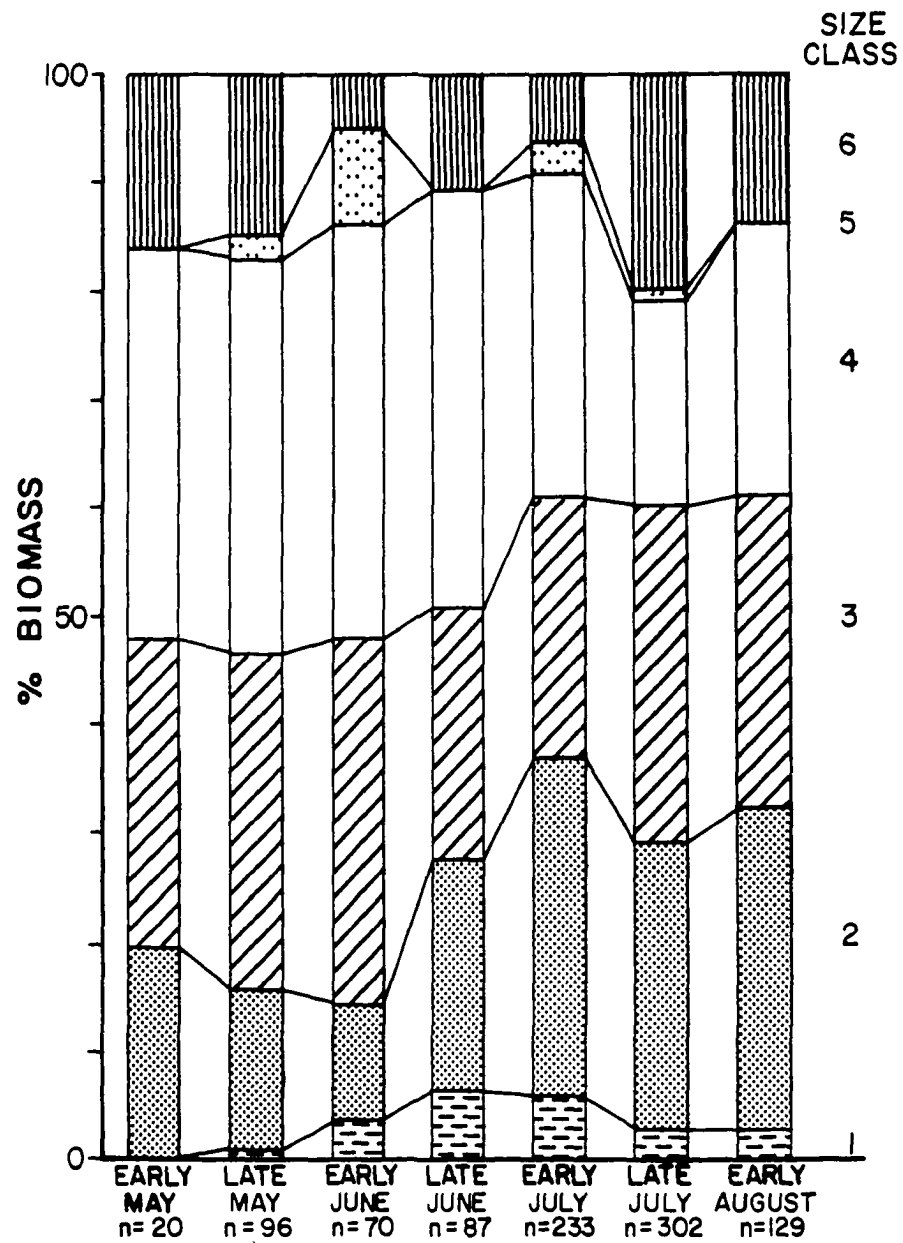Figure 14. Mean weight of sharp-shinned hawk prey through the breeding season, interior Alaska, 1978-1981.

Figure 15. Size class (Storer 1966) composition of sharp-shinned hawk prey through the breeding season, interior Alaska, 1978-1981.

insects. For example, at both Campus nest sites, hawks used the same broken white spruce tor a plucking perch. The tree was inhabited by carpenter ants (Camponotus sp.), and many ants appeared in the castings collected at the sites. It could be that passerines were eating ants at the perch when they themselves were captured and eaten by hawks, but I feel that it is more likely that the hawks caught the ants themselves.

The undigestible non-prey items found in pellets (i.e., spruce needles, twigs, bracts, etc.) were probably ingested incidentally while dismembering prey on the ground, when forest litter adhered to the prey and was consumed. The size and number of fragments indicate that perhaps eggshells were intentionally broken up and swallowed.

Compared with other studies (e.g., Fisher 1893, Bent 1937, Munro 1940, Craighead and Craighead 1956, Storer 1966, Snyder and Wiley 1976, Reynolds 1978, Duncan 1980), this assessment of sharp-shinned hawk diet presents few surprises. One unusual aspect of these data is that a relatively large portion of the diet, 3.94% by biomass, is comprised of bank swallows (Riparia riparia), a species well-known for its ability to avoid raptor attacks by mobbing would-be predators (Hoogland and Sherman 1976). Even away from the protection of the flock, single bank swallows would be difficult, evasive targets for sharp-shinned hawks, yet they appear frequently in the hawks' diet. In 1980, D. G. Roseneau (pers. comm.) observed an adult male sharp-shinned hawk perched at the entrance of a bank swallow nest burrow on the Tanana

River, apparently searching for prey. In 1982 and 1983, I observed adult female sharp-shins in similar situations, and this behavior has also been reported for American kestrels (Freer 1973, R. B. Weeden pers. comm.). Burrow-searching may be an effective means by which sharp-shinned hawks capture this otherwise elusive prey, and it could account for the seemingly disproportionately high incidence of bank swallows in my prey samples.

Surprisingly, I found the remains of a saw-whet owl (Aegolius acadicus) in the stomach of a window-killed sharp-shinned hawk from Petersburg, Alaska. The owl was not included with previous discussion because the hawk that ate it was found dead in mid-winter in an area well away from and quite unlike the study area, yet it is worth noting to re-emphasize the opportunistic nature of these hawks. Apparently, G. E. Lodge's comment on European sparrowhawks, "they'd kill cows if they could" (Mavrogordato 1973) applies equally well to sharp-shinned hawks in Alaska.

PREY ABUNDANCE

Songbird abundance data compiled by other researchers (West and DeWolfe 1974, Spindler 1976, Spindler and Kessel 1980) were collected in habitats similar to my study area, but in years other than those in which prey remains were collected, so it is not valid to compare them closely with my findings. Still, since values from different studies in different years correspond to some degree, I suspect that rankings of bird species by relative abundance are generally applicable (Table

27).

Sharp-shinned hawks in Alaska, like those in Oregon (Reynolds 1978), capture prey in roughly the same proportions in which they exist in the wild. Of the ten most abundant prey species, seven were among the top ten prey species according to biomass (Tables 24 and 27).

Because none of the sources of songbird abundance data included all three Catharus species in their surveys, Catharus thrush abundance estimates may be artificially low. Catharus thrushes appear to be taken preferentially, since they appear in the prey samples more frequently than would be expected if they were taken only in proportion to their availability (Figure 16). Indeed, Catharus thrushes would seem to be preferable to other prey, as they are of an optimal size (Storer 1966), have a slightly higher caloric value than other songbirds (Cummins and Wuycheck 1971), and are consistently abundant from year to year (Spindler and Kessel 1980).

It is possible that hawks prefer to hunt in forest habitats, and consequently, take many forest-dwelling prey and relatively few open-country birds (Table 28). For example, yellow warblers and yellow-rumped warblers are eaten more frequently than their availability might lead one to predict (Figure 16). Both species inhabit mixed, often patchy, forest with an open understory (Spindler 1976, Spindler and Kessel 1980). Such habitat would provide canopy cover to conceal a hunting hawk, but little cover for warblers. This would be more likely for yellow warblers, which forage in the upper shrub/lower canopy zone,

Table 27. Relative abundance by percent biomass of selected avian species, after West and DeWolfe (1974), Spindler (1976) and Spindler and Kessel (1980).

Species	West and DeWolfe Trail "A"	Trail "B"	Spindler	Spindler and Kessel	$\bar{X}$	z^3	S.D.
American robin	25.5	24.6	1.3	30.1	20.4	16.7	12.9
dark-eyed junco	11.8	24.6	12.0	3.2	12.9	10.5	8.8
Swainson's thrush and/or gray-cheeked thrush	9.8	15.5	6.6	18.5	12.6	10.3_1	5.4
common snipe	-	-	11.7	-	11.7	$-_1$	0.0
white-crowned sparrow	10.3	-	9.1	10.5	10.0	8.2	0.8
fox sparrow	12.0	-	4.7	12.6	9.8	8.0_1	4.4
mew gull	-	-	8.6	-	8.6	-	0.0
varied thrush	4.5	11.8	-	6.7	7.7	6.3	3.7
American tree sparrow	-	-	7.0	-	7.0	5.7	0.0
redpoll sp.	8.2	5.4	3.1	-	5.6	4.6	2.6
Lincoln's sparrow	0.3	-	10.2	-	5.3	4.3	7.0
yellow-rumped warbler	3.2	9.5	2.1	3.0	4.5	3.7_1	3.4
gray jay	-	-	4.1	-	4.1	$-_1$	0.0
rusty blackbird	2.4	-	5.3	-	3.9	3.2	2.1
northern waterthrush	-	-	2.6	4.2	3.4	2.8	1.1
yellow warbler	2.6	-	2.4	4.6	3.2	2.6	1.2
lesser yellowlegs	2.1	-	4.2	-	3.2	2.6	1.5
Bohemian waxwing	-	-	2.4	-	2.4	2.0	0.0
Townsend's warbler	0.6	3.6	-	-	2.1	1.7	2.1
orange-crowned warbler	1.1	2.4	0.2	2.2	1.5	1.2	1.0
savannah sparrow	0.5	-	-	2.1	1.3	1.1	1.3
Hammond's flycatcher	1.2	-	-	1.1	1.2	1.0_1	0.1
pine grosbeak	-	-	1.1	-	1.1	$-_1$	0.0

Table 27. (continued)

Species	West and Trail "A"	DeWolfe Trail "B"	Spindler	Spindler and Kessel	$\bar{x}$	$\%^3$	S.D.
ruby-crowned kinglet	1.0	1.4	–	0.7	1.0	0.8	0.4
black-capped chickadee	1.0	–	–	–	1.0	0.8	0.0
alder flycatcher	0.9	1.3	0.3	–	0.8	0.7	0.5
boreal chickadee	–	–	0.7	–	0.7	0.6	0.0
Wilson's warbler	0.4	–	–	0.6	0.5	0.4	0.1
blackpoll warbler	–	–	0.3	–	0.3	0.2	0.0
	100.1	100.1	100.1	100.0	122.3[2]	100.0	

[1]Not identified as sharp-shinned hawk prey.

[2]Total indicates species identified as sharp-shinned hawk prey only.
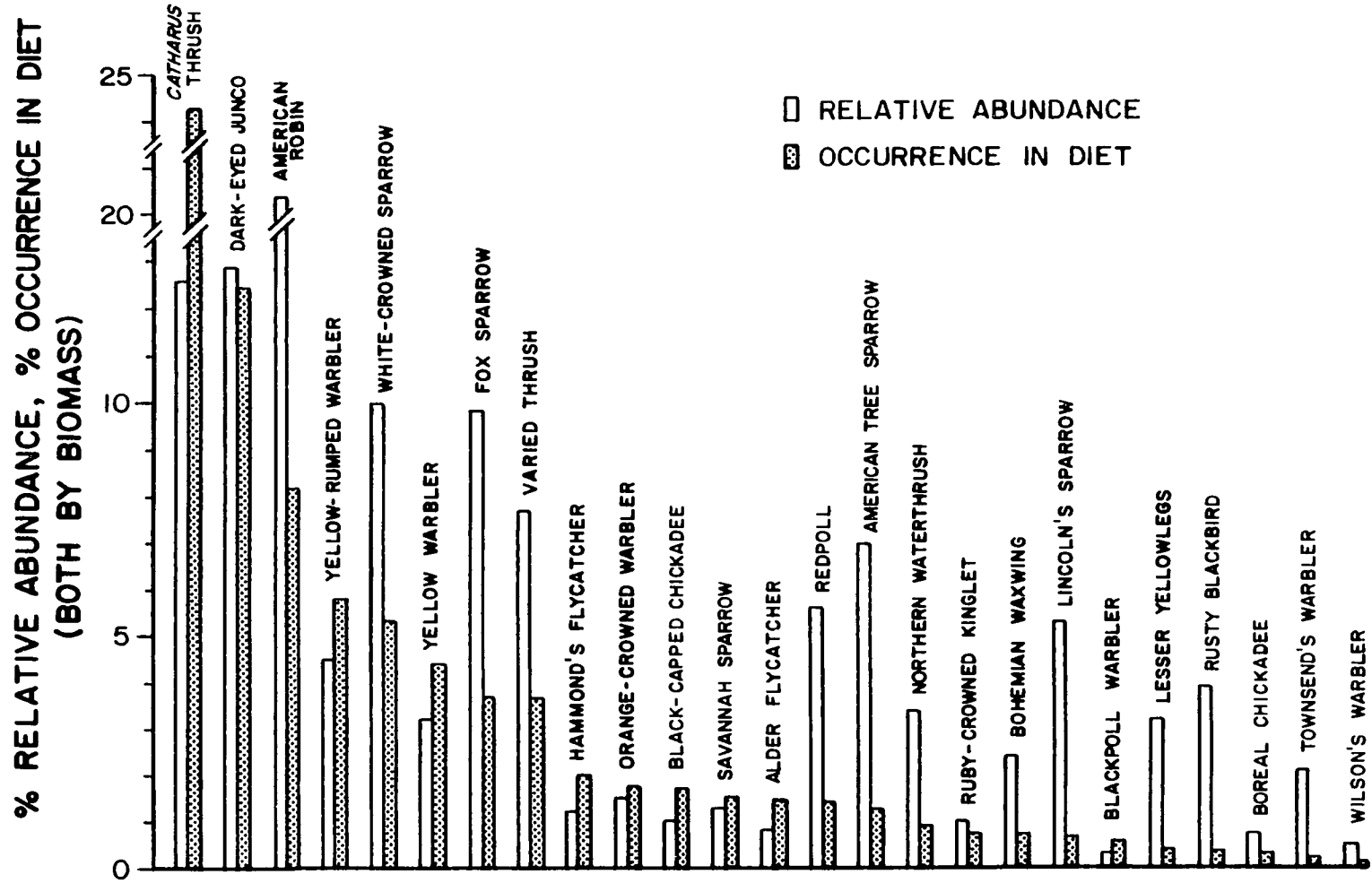
[3]Percentage of [2].

Figure 16. Relative abundance vs. occurrence in sharp-shinned hawk diet of selected avian species, interior Alaska, 1978-1981.

Table 28. Occurrence in diet and relative abundance of selected sharp-shinned hawk prey species, according to habitat type as described by Spindler and Kessel (1980).

Habitat Type	Percent of Diet by Biomass (Relative Percent)[1]	Avian Prey Availability[2]
Open Shrub Thicket (white-crowned sparrow, savannah sparrow, American tree sparrow, northern waterthrush, Lincoln's sparrow, lesser yellowlegs, rusty blackbird)	10.4 (14.0)	27.9
Closed Tall Shrub Thicket (yellow warbler, fox sparrow, alder flycatcher, blackpoll warbler)	10.1 (13.6)	11.5
Open Forests and Scattered Woodlands (American robin, orange-crowned warbler, redpoll sp., Bohemian waxwing)	12.0 (16.2)	24.5
Mature Forest	41.1 (55.5)	33.3
Coniferous (ruby-crowned kinglet)	(0.7) (0.9)	(0.8)
Deciduous (hermit thrush, yellow-rumped warbler, Hammond's flycatcher, black-capped chickadee)	(9.5) (12.8)	(5.5)
Mixed (dark-eyed junco, Swainson's or gray-cheeked thrush, varied thrush, Wilson's warbler)	(16.1) (21.7)	(27.0)
Fully-developed Coniferous Forest (boreal chickadee, Townsend's warbler)	0.5 (0.7)	2.3
TOTAL	74.1[3] (99.8)	99.5

[1] Table 23
[2] Table 27
[3] <100% because abundance figures not available for all prey species

than for yellow-rumped warblers, which forage in the upper canopy. A preference of the hawks to hunt from cover of the forest canopy might also explain why they take comparatively few American robins, white-crowned sparrows, redpolls, American tree sparrows, Lincoln's sparrows, lesser yellowlegs and rusty blackbirds. These species inhabit open habitat, often with little or no canopy cover (Spindler 1976, Spindler and Kessel 1980).

Perhaps because redpolls maintain loose flocks through the breeding season (D. M. Troy, pers. comm.), they occur less frequently in the diet than expected (Figure 16). Hawks approaching flocks might be detected sooner and avoided more frequently than are hawks approaching single birds (Page and Whitacre 1975).

The rate of sharp-shinned hawk predation upon the most commonly eaten prey species (Catharus thrush and dark-eyed junco) was relatively constant through the breeding season (Figure 17). This is not the case with some other species (Figure 17). There are several possible explanations for such differential use. For example, white-crowned sparrows, fox sparrows and varied thrushes are eaten relatively infrequently (Figure 16), perhaps because they usually remain near cover. However, during the early stages of the breeding season, cover is sparse and territorial males display in ways which render them visible, perhaps more vulnerable to attack. If this were true, individuals of these three species, especially males, should be taken most frequently during the first weeks of the breeding season and, indeed, this appears
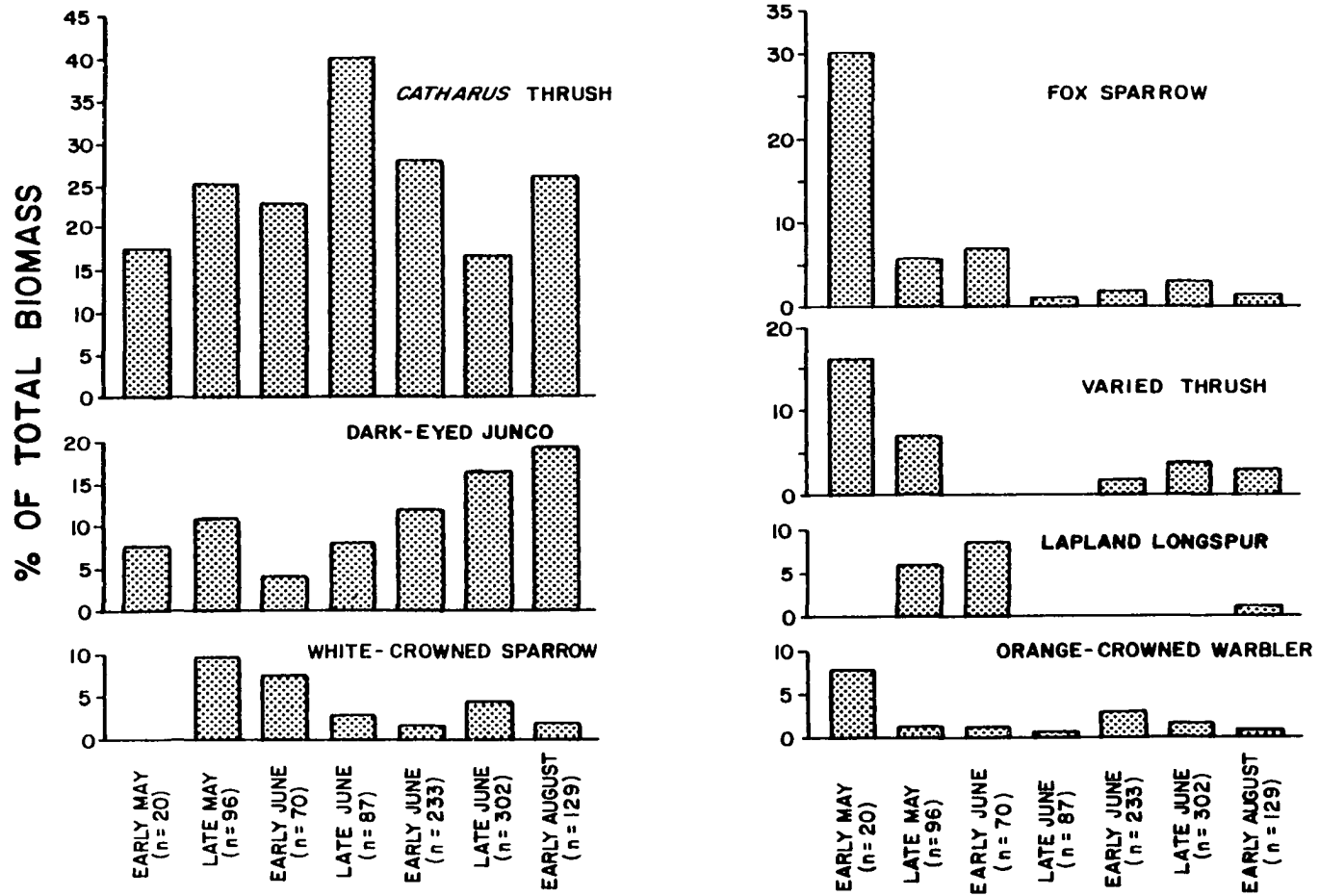
Figure 17. Changes through the breeding season in relative occurrence in sharp-shinned hawk diet of selected avian species, interior Alaska, 1978-1981.

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to be the case (Figure 17). This applies as well to orange-crowned warblers (Figure 17).

Lapland longspurs are transients, available only early in the season and again late in the summer. The pattern of use by sharp-shinned hawks clearly reflects this disparity in abundance through the season (Figure 17).

HUNTING HABITAT AND FORAGING STRATEGY

Sharp-shinned hawks rely on species from mature forest habitats for at least half of that portion of their diet which can be categorized as to habitat type (Table 28). A corollary to this is that sharp-shinned hawks probably spend a corresponding amount of time hunting in mature forest habitats. They probably venture frequently into shrub thickets to hunt (species accounting for nearly 20% of their diet by biomass inhabit open or closed shrub thickets), but spend little time hunting in the less diverse fully-developed coniferous forest (less than 1% of their diet is comprised of birds from these habitats). While it is reasonable to assume that sharp-shinned hawks prey upon avian species in roughly the same proportions in which they occur, it is equally reasonable to assume that these hawks are not searching for food in an entirely random fashion. They seemed to concentrate their hunting efforts in the habitat with the greatest diversity and second-greatest abundance of avian prey (Spindler and Kessel 1980), while avoiding the more open habitats and the relatively barren conifer forest.

There are several possible explanations for this apparent selective use of habitat. Perhaps sharp-shinned hawks nest where middle-aged conifers provide appropriate bases for nest construction; i.e., the hawks hunt to a large extent where they build their nests. Conversely, they may place their nests in the most productive hunting grounds, which incidentally contain a few trees of appropriate structure for nest building. It could also be that the hawks have adopted a strategy which optimizes their foraging effort, an hypothesis which merits further exploration.

Sharp-shinned hawks apparently did not concentrate their hunting efforts in any particular vegetation height zone, but adhered to the pattern of taking prey according to its availability. Hawks took nearly 65% of their prey by biomass from cohorts of prey which are found either generally throughout the vegetation column or in the lowest portion of the vegetation regime; these two zones include nearly 74% of the available prey (Table 29). This is in direct contrast to the findings of Reynolds (1978), who reported that sharp-shinned hawks in Oregon did most of their hunting in the mid- to upper-canopy zone. This is at least partially due to a disparity in relative abundance and/or habits of prey species between Oregon and Alaska, but I do not concur with Reynolds' conclusion that "... _Accipter striatus_, a prey size specialist, was necessarily a zone and guild specialist." Interior Alaska sharp-shinned hawks are indeed prey size specialists, but this forces them to be "opportunistic generalists", since small birds in the

Table 29. Occurrence in diet and relative abundance of sharp-shinned
hawk prey species according to foraging zone and guild
affiliations, interior Alaska, 1978-1981.

	% Biomass in Diet	Avian Prey Availability[2]
Foraging Zone[1]		
Ground-Lower Shrub	39.6	35.0
Upper Shrub-Lower Canopy	13.9	18.4
Upper Canopy	10.9	7.9
Aerial	4.5	----
Generalists	25.4	38.7
unidentified	5.8	----
	100.1	100.0
Foraging Guild[1]		
Ground Searchers	31.5	46.4
Trunk Gleaners	0.1	----
Foliage Gleaners	11.9	4.0
Hawkers	4.1	1.7
Aerial Insectivores	4.5	----
Generalists	41.9	47.9
unidentified	6.1	----
	100.1	100.0

[1]After Reynolds (1978; see Table 22)
[2]Relative abundance of those species listed in Table 27 known to be
taken as sharp-shinned hawk prey (adults only)
---- no data

interior are distributed throughout the zone and guild spectra.

The occurrence of mammals in the diet probably reflects the opportunistic nature of the sharp-shinned hawk hunting rather than a concerted effort to capture mammalian prey. Reynolds (1978) surmised that the sharp-shinned hawks he studied captured few mammals because the hawks foraged primarily in the upper canopy zone and simply did not encounter small mammals. This explanation does not hold true for the hawks in this study, which did forage near the ground, and did encounter and capture ground-dwelling mammals (Table 24).

ENERGY REQUIREMENTS

I estimated the total energy required by a typical family of sharp-shinned hawks during one complete breeding season (1 May to 1 September) according to Reynolds (1978), given the following:

where W = body weight

M_{30} = daily existence energy (at $30^{o}C$)

EW = egg weight

EC = energetic demand for producing a clutch of eggs

NS = average brood

NP = nestling period

FS = average number of fledglings

FP = fledgling period

PP = post-fledging period

MN = energetic cost of nestling growth

MF = fledgling daily existence energy

MP = post-fledging daily existence energy

$M_{30} = 0.5404 \ (W)^{0.7545}$

W = 103.2 g (male), 199.1 g (female)

$EW = 0.741 \ (W_{female})^{0.633}$

CS = 5.1 eggs

NS = 4.4 nestlings

NP = 24 days

FS = 3.1 fledglings

FP = 25 days

PP = 11 days

$M_{30}male = 0.5404 \ (103.2)^{0.7545}$ kcal = 20.8 kcal

$M_{30}female = 0.5404 \ (199.1)^{0.7545}$ kcal = 34.1 kcal

$\overline{X}M_{30}adult = (20.8 + 34.1)/2$ kcal = 27.5 kcal

$M_{male} = 20.8 \ (1.43) \ (1.4) \ (123 \ days)$ kcal = $\underline{5121.9 \ kcal}$

$M_{female} = 34.1 \ (1.43) \ (1.4) \ (123 \ days)$ kcal = $\underline{8397.0 \ kcal}$

$EW = 0.741 \ (199.1)^{0.633} = 23.6$ g

EC = 23.6 (5.1) (1.05) (1.37) kcal = 173.1 kcal

$MN = \overline{X}M_{30}adult \ (1.20) \ (1.43) \ (4.4) \ (24)$ kcal = $\underline{4983.3 \ kcal}$

$MF = \overline{X}M_{30}adult \ (1.15) \ (1.43) \ (3.1) \ (25)$ kcal = $\underline{3504.8 \ kcal}$

$MP = \overline{X}M_{30}adult \ (1.43) \ (3.23) \ (11)$ kcal = $\underline{1397.2 \ kcal}$

Two potential sources of inaccuracy can be removed by substituting observed values for calculated:

$EW_{observed} = 20.0$ g (n = 14) (Figure 6), so

EC = 20.0 (5.1) (1.05) (1.37) kcal = $\underline{146.7 \ kcal}$

average food intake of hand-reared young to reach maximum weight was

680 g, so

MN = 680 (1.757 kcal/g) (4.4) kcal = 5256.9 kcal

Thus,

$M_{male} + M_{female}$ + EC + MN + MF + MP = total energy requirement, or

5121.9 + 8397.0 + 146.7 + 5256.9 + 3504.8 + 1397.2 = 23,824.5 kcal

Assuming that 96.9% of the total weight represented by this figure
is avian biomass (1.757 kcal/g) and 3.15% is mammalian (1.501 kcal/g)
(Table 24), 23,824.5 kcal is equivalent to 13,620.8 g of prey, or 728
prey animals (Table 30).

IMPACT ON PREY POPULATIONS

The influence of sharp-shinned hawks is an important consideration
for anyone estimating numbers of birds in interior Alaska. In two sur-
veys through the breeding season, interior Alaska taiga was estimated
to contain an average of 326.6 birds of 22 species and 121.6 birds of
10 species per 100 ha (West and DeWolfe 1974). According to these
estimates, a 379.9 ha sharp-shinned hawk home range (Table 12) would
contain at least 1240.8 and 462.0 birds. Removal of 711 birds (Table
30) would constitute a major impact on either population. Such an in-
fluence has never been considered by previous investigators.

I found six old nests near West and DeWolfe's (1974) study "trail
B". If one of those nests were active during the survey year, it might
explain why there were fewer birds detected along "trail B" than "trail
A". A sharp-shinned hawk was seen during the survey period, but it is

Table 30. Hypothetical diet of a typical interior Alaska sharp-shinned hawk family from spring arrival through fall departure, 1 May to 1 September.

Species	Biomass (g)	Number
<u>Catharus</u> thrush	3305.5	127
dark-eyed junco	1692.2	98
American robin	1113.6	14
yellow-rumped warbler	785.5	67
white-crowned sparrow	721.5	33
yellow warbler	600.4	66
bank swallow	536.4	34
fox sparrow	498.3	15
varied thrush	496.9	7
unidentified (Class 1, 2, 3, or 4)	299.5	18
Hammond's flycatcher	268.2	27
orange-crowned warbler	239.6	28
black-capped chickadee	232.8	21
unidentified (Class 2 or 3)	226.0	16
savannah sparrow	209.7	12
Lapland longspur	206.9	8
alder flycatcher	200.1	17
redpoll	192.0	15
American tree sparrow	174.3	10
unidentified (Class 3)	138.9	8
northern waterthrush	119.8	7
ruby-crowned kinglet	98.0	15
Bohemian waxwing	93.9	1
Lincoln's sparrow	89.9	6
unidentified (Class 2)	81.7	7
blackpoll warbler	74.9	7
western wood-pewee	68.1	6
solitary sandpiper	65.3	1
lesser yellowlegs	50.4	1
rusty blackbird	46.3	1
tree swallow	44.9	2
boreal chickadee	40.8	3
Townsend's warbler	27.2	3
cliff swallow	24.5	1
unidentified (Class 4 or 5)	24.5	1
spotted sandpiper	23.1	1
olive-sided flycatcher	21.8	1
unidentified (Class 1 or 2)	19.1	2
downy woodpecker	16.3	1

Table 30. (continued)

Species	Biomass (g)	Number
Wilson's warbler	10.9	1
pine siskin	8.2	1
unidentified (Class 1)	4.1	1
Total Birds[1]	13192.0	711
northern red-backed vole	284.5	11
snowshoe hare	57.2	1
unidentified mammals	40.8	2
meadow jumping mouse	23.1	1
meadow vole or tundra vole	19.1	1
shrew	4.1	1
Total Mammals[2]	428.8	17
TOTAL	13620.8	728

[1]Assuming 93.44% adult/immature, 5.99% juvenile, 0.58% nestling (Table 24).

[2]Assuming all adult, except snowshoe hares assumed to be juvenile.

not known if or where it was nesting.

The hypothetical statewide impact of sharp-shinned hawks on avian numbers is awesome. Alaska contains from 43 to 60 million ha of taiga (Viereck 1973). At a density of 23.8 pairs per 100 km^2 (Table 13), this expanse of boreal rorest could support 102,340 to 142,800 breeding pairs of sharp-shinned hawks. Those sharp-shinned hawk families would consume 72.8 to 101.5 million songbirds in one breeding season.

SUMMARY

Sharp-shinned hawks arrived on the breeding grounds by early May. Birds not already paired found mates and began the nesting effort quickly. Courtship was brief. Most pairs (57%) were both adults, although 36% of females were in brown immature plumage. Breeding females molted rapidly until the mid-nestling phase, when the molt was arrested. Males molted very slowly through the entire breeding season. Males provided food and females tended eggs or young. Both sexes defended the nest site.

Sharp-shinned hawks commonly re-used past nesting areas. Nests were built in conifers, usually white spruce, within a matrix of mixed deciduous and coniferous trees. Nest sites were dominated by densely-packed young trees; canopy and ground cover were extensive. Nest trees tended to be older, larger individuals. Nests were large, bulky platforms built of twigs, and were usually placed on the southerly half of the nest tree trunk. Some nests were built between the trunks of two or more closely-spaced trees. Clumps of bent-over willows, fallen trees, logs and stumps were used as plucking perches, often from year to year, even though birds almost always built a new nest each year.

Sharp-shinned hawks, especially males, vigorously attacked intruders at nest sites. Radio telemetry showed that one pair occupied a 380 ha home range. Nesting density was estimated at 23.8 pairs per 100 km^2, much greater than estimates for sharp-shinned hawks elsewhere. Females laid eggs every other day, beginning in mid- to late May, with

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incubation beginning with the laying of the last egg. Eggs were slightly larger but had thinner shells than other eggs studied. Females carried out all of the incubation, while males provided food through incubation and into the mid-nestling period, when females began to hunt again. Eggs hatched synchronously and young grew rapidly, fledging in 23-26 days. Males developed muscular coordination and motor skills faster than females, which gained weight and increased in body size more quickly. Captive-reared and wild hawks grew at similar rates, but captive birds attained greater weights and larger body sizes. Captive-reared hawks showed very efficient rates of conversion of food to body tissue. After fledging, adults spent less time in the immediate vicinity of the nest. Young birds strayed further and further from the nest, returning only to be fed. Young chased prey as early as seven days after fledging.

Sharp-shinned hawks laid an average of 5.1 eggs per nest, of which 4.4 hatched, with 3.1 young fledging successfully. All of these figures are greater than reported for sharp-shins studied elsewhere.

Mortality rates are poorly known. Some nestlings and fledglings were apparently taken by other predators, and evidence was found to suggest that accidental death, especially due to collisions with windows, is common.

Family units break up and birds disperse 20-25 days post-fledging. Birds then apparently moved along with passerines on southward migration.

Analysis of prey remains showed a diet of 97% small birds and 3% small mammals by biomass. Sharp-shinned hawks captured prey in proportion to its availability, but apparently spent more time hunting in the most productive habitat types rather than foraging at random.

The total energy requirement of a typical sharp-shinned hawk family for the entire breeding season was estimated to be 13,260 g, equivalent to about 711 small birds and 17 small mammals. Removal of prey at that rate from a relatively small home range constitutes a significant impact on songbird populations, an impact which has heretofore gone totally unnoticed.

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