Aspects of the Nutritional Ecology of the Red-shouldered Hawk (*Buteo lineatus lineatus*) in southwestern Quebec.

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A thesis submitted to the Faculty of Graduate Studies and Research of McGill University in partial fulfillment of the requirements for the degree of Master of Science.

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Abstract

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Aspects of the Nutritional Ecology of the Red-shouldered Hawk (Buteo lineatus lineatus) in southwestern Quebec

Red-shouldered Hawks were studied for two seasons to determine the diet composition and to measure the effect of brood size on the feeding frequency by the parents. Some aspects of their growth were quantified and the effect of brood size on the growth of specific body parameters and forms of nest attendance were studied.

Adults brought a wide variety of prey items to the nestlings with significantly more mammal prey delivered in 1980 than in 1979. This annual variation of the two main prey types may be related to winter weather conditions prior to each nesting season. The total weight of prey delivered in the 4-hour observation blocks was negatively correlated with the number of prey deliveries in small (1 or 2 young) and large (3 or 4 young) broods. Larger broods received significantly more prey than smaller broods. However, individuals of the largest natural brood size (4 young) were not fed as much as individuals of the most common brood size (3 young).

The growth of bill, tarsus and tail feather length were significantly different in broods of 3 compared to broods of 1. Some interaction between brood size and age accounted for the first two differences, whereas brood size alone was responsible for the differences in tail feather growth between the brood sizes. No difference was found for wing feather growth or weight gain between the two brood sizes.

Nest attendance in terms of frequency of brooding and delivery of greenery to the nest, was greater in broods of 3 compared to broods

of 1.

A combination of increased brooding, delivery of greenery and prey in broods of 3 compared to broods of 1, probably accounted for the differences in growth of certain body parameters.

Résumé

M.Sc. Brenda L. Penak Département des Ressources Renouvelables

Des Aspects de L'Ecologie Nutritional de la Buse à Epaulettes Rousses (Buteo lineatus lineatus) dans le sud-ouest du Québec

Pendant deux saisons, on a étudié les Buses à épaulettes rousses dans le but de déterminer la composition de leur régime alimentaire ainsi que d'évaluer la grandeur des couvées par rapport à la fréquence de l'alimentation parentale. Certains aspects de leur croissance ont été quantifiés. En plus, les effets de la grandeur des couvées sur la croissance des paramètres corporels spécifiques et la fréquentation au nid ont été étudies.

L'apport des proies par les parents a montré une grande variété, avec une nette augmentation de mammifères pour 1980 par rapport à 1979. La différence constatée entre ces deux dernières années peut être reliée aux conditions hivernales qui précedent la nidification. Le poids total des proies rapportées au nid au cours de la période d'observation de quatre (4) heures a correspondu négativement avec le nombre de proies rapportées aux petites couvées (un ou deux jeunes) et aux grandes couvées (trois ou quatre jeunes). Les grandes couvées ont reçu une quantité plus importante de proie que les petites couvées. Cependant, les oisillons de la couvée la plus grande (quatre jeunes) n'ont pas reçu autant de nourriture que les oisillons des couvées de la grandeur la plus commune (trois jeunes).

La croissance du bec, du tarse ainsi que la longeur de la penne rectrice était considérablement différente chez les couvées de trois individus comparativement aux couvées d'un seul oisillons. L'interaction entre la grandeur de la couvée et l'âge des oisillons expliquait les

les deux premières différences (c'est-à-dire, la croissance du bec et du tarse) tandis que la grandeur des couvées, seule, expliquait la différence de croissance de la penne rectrice dans le couvées de différentes grandeurs. Aucune différence n'a été constatée entre les deux grandeurs des couvées en ce qui concernaient la croissance des plumes des ailes et l'augmentation de poids.

La fréquentation au nid, dans le sens de fréquence de couvaison ainsi que le renouvelement de végétation dans le nid, était plus importante chez les couvées de trois oisillons par rapport à celles d'un seul.

Il est probable qu'une plus longue période de couvaison, jumelée à un apport plus grande de proie et de végétation, expliquent les différences de croissance de certains paramètres corporels chez les couvées de trois jeunes par rapport à celles d'un seul oisillon.

Preface

Part I of this thesis was concerned with the determination of the diet in Red-shouldered Hawks and the effect of brood size on the feeding frequency of the parents. This was accomplished by recording observations at nests and collecting and analysing pellets in both 1979 and 1980.

Part II of this thesis aimed to determine the effect of feeding frequency and parental care on growth of different broods. This was accomplished by continuing behavioural observations as well as measuring young of selected nests with different brood sizes every 4 to 7 days.

Based on the results of behavioural observations conducted during the first year of the study, new predictions involving growth and the effect of brood size were generated. The first paper therefore served as a basis for the second one.

Since the quantification of growth data for raptors has not been discussed extensively in the literature, it was felt that the uniqueness of the data should be emphasized. Therefore, the growth analysis was presented as a paper on its own.

In general, data collected for the thesis were divided into two parts based on the year the information was gathered. A sufficient sample size and range of brood sizes facilitating the analysis of growth data were collected only for 1980. However, diet information was accumulated for both study years. This naturally lent itself to the separation of the thesis into two papers.

Abstract
Part I

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Dietary composition and frequencies of prey delivery in Red-shouldered Hawk (Buteo lineatus) broods in southwestern Quebec.

Red-shouldered Hawks were studied for two seasons to determine the diet composition and to measure the effect of brood size on the feeding frequency by the parents.

Adults brought a wide variety of prey items to the nestlings with significantly more mammal prey delivered in 1980 than in 1979. This annual variation of the two main prey types may be related to winter weather conditions prior to each nesting season. The total weight of prey delivered in the 4-hour observation blocks was negatively correlated with the number of prey deliveries in small (1 or 2 young) and large (3 or 4 young) broods. Larger broods received significantly more prey than smaller broods. However, individuals of the largest natural brood size (4 young) were not fed as much as individuals of the most common brood size (3 young).

Résumé
Première Partie

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La composition alimentaire de proie et les fréquences de son apport chez les couvées de la Buse à épaulettes rousses (Buteo lineatus) dans le sud-ouest du Québec

Pendant deux saisons, on a étudié les Buses à épaulettes rousses dans le but de déterminer la composition de leur régime alimentaire ainsi que d'évaluer la grandeur des couvées par rapport à la fréquence de l'alimentation parentale.

L'apport des proies par les parents a montré une grande variété, avec une nette augmentation de mammifères pour 1980 par rapport à 1979. La différence constatée entre ces deux dernières années peut être reliée aux conditions hivernales qui précedent la nidification. Le poids total des proies rapportées au nid au cours de la période d'observation de quatre (4) heures a correspondu négativement avec le nombre de proies rapportées aux petites couvées (un ou deux jeunes) et aux grandes couvées (trois ou quatre jeunes). Les grandes couvées ont reçu une quantité plus importante de proie que les petites couvées. Cependant, les oisillons de la couvée la plus grande (quatre jeunes) n'ont pas reçu autant de nourriture que les oisillons des couvées de la grandeur la plus commune (trois jeunes).

Abstract
Part II

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The relationship of brood size to parental care and growth of nestling Red-shouldered Hawks (Buteo lineatus) in southwestern Quebec.

Some aspects of the growth of Red-shouldered Hawks were quantified and the effect of brood size on the growth of specific body parameters and forms of nest attendance were studied.

The growth of bill, tarsus and tail feather length were significantly different in broods of 3 compared to broods of 1. Some interaction between brood size and age accounted for the first two differences, whereas brood size alone was responsible for the difference in tail feather growth between the brood sizes. No difference was found for wing feather growth or weight gain between the two brood sizes.

Nest attendance, in terms of frequency of brooding and delivery of greenery to the nest, was greater in broods of 3 compared to broods of 1.

A combination of increased brooding, delivery of greenery and prey (Part I) in broods of 3 compared to broods of 1, probably accounted for the differences in growth of certain body parameters.

Résumé
Deuxième Partie

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La croissance de la jeune Buse à épaulettes rousses (Buteo lineatus) dans le sud-ouest du Québec et le rapport entre la grandeur des couvées et les soins parentaux

Certains aspects de la croissance des Buses à épaulettes rousses ont été quantifiés. En plus, les effets de la grandeur des couvées sur la croissance des paramètres corporels spécifiques et la fréquentation au nid ont été étudiés.

La croissance du bec, du tarse ainsi que la longeur de la penne rectrice était considérablement différente chez les couvées de trois individus comparativement aux couvées d'un seul oisillon. L'interaction entre la grandeur de la couvée et l'âge des oisillons expliquait les deux premières différences (c'est-à-dire, la croissance du bec et du tarse) tandis que la grandeur des couvées, seule, expliquait la différence de croissance de la penne rectrice dans le couvées de différentes grandeurs. Aucune différence n'a été constatée entre les deux grandeurs des couvées en ce qui concernaient la croissance des plumes des ailes et l'augmentation de poids.

La fréquentation au nid, dans le sens de fréquence de couvaison ainsi que le renouvelement de végétation dans le nid, était plus importante chez les couvées de trois oisillons par rapport à celles d'un seul.

Il est probable qu'une plus longue période de couvaison, jumelée à un apport plus grande de proie et de végétation (première partie), expliquent les différences de croissance de certains

paramètres corporels chez les couvées de trois jeunes par rapport à celles d'un seul oisillon.

Table of Contents

	Page
Acknowledgements	ix
List of Figures	xi
List of Tables	xii
List of Appendices	xiii
Part I Dietary Composition and Frequencies of Prey Delivery in Red-shouldered Hawk (Buteo lineatus) Broods, in Southwestern Quebec	1
1. Introduction	2
2. Study Area	3
3. Materials and Methods	5
3.1 Data Analysis	8
4. Results	8
4.1 General Diet	8
4.2 Prey Size and Frequency of Prey Delivery	9
5. Discussion	17
5.1 General Diet	17
5.1.1. Observations	17
5.1.2. Pellet Analysis	19
5.2 Prey Size and Frequency of Prey Delivery	20
6. Conclusions	23
Literature Cited	25
Part II The Relationship of Brood Size to Parental Care and Growth of Nestling Red-shouldered Hawks (Buteo lineatus) in Southwestern Quebec	31
1. Introduction	32
2. Study Areas	33

Page

3. Materials and Methods..... 34

3.1 Data Analysis..... 37

4. Results..... 38

5. Discussion..... 44

6. Conclusions..... 46

Literature Cited..... 47

Acknowledgments

This thesis is dedicated to the memory of Jo Wright, a good friend and an outstanding naturalist, who provided invaluable field assistance and nesting data on Red-shouldered Hawks in southwestern Quebec.

My supervisor, Dr. David Bird is thanked for allowing me the opportunity to work on this species and for providing financial assistance through the Macdonald Raptor Research Centre of McGill University. He is also thanked for his helpful comments, his editorial and field assistance. Drs. Rodger Titman, Paul Laguë and Robert Lemon are acknowledged for their advice during one or more stages of the project. I would also like to extend my appreciation to Dr. Jim Mosher, formerly of the University of Maryland for his very useful suggestions throughout the study.

Bob Clark is especially thanked for his advice during the study and his invaluable assistance with the computer analysis. Roger Belanger, Jean Phaneuf and Tom Clark are also thanked for their help with the statistical analysis as well as their thought-provoking discussions.

Many people who aided in the field work at one time or another are gratefully acknowledged: Grant Bracher, Dave Gordon, Hamilton Greenwood, Guy Huot, Alison Lemay, Claire Masari, Laura Mauro, Nancy Rehder, Ian Ritchie, Laird Shutt, Joyce Snyder, Steve Tinker, Peter Tucker, Dr. Patrick Weatherhead and Mark Wayland. Bruce Lyon and Albert Kuhnigk are specially thanked for providing information on old nests as well as searching for new nests. Much debt is

owed to Johnny Watson who provided tree-climbing services during the first field season. In the second field season he kindly loaned his climbing gear and trained another brave individual in the art of climbing.

I would like to express my extreme gratitude to those who contributed much time and effort in both the field and technical aspects of this study: Kim Asquith, David Lemon, Michael Morris and Dr. Glenda M. Wright.

Delise Alison, of the Redpath Museum of McGill is thanked for kindly providing laboratory space and access to museum specimens.

Dr. Henri Ouellet, of the National Museum of Natural History in Ottawa, is also acknowledged for providing access to study specimens.

Alison Bently and family, of Rigaud Mt. are thanked for their frequent hospitality to the author and fellow workers during the field seasons.

Jan Qualtrough who kindly and quickly typed this thesis, Wayne Berry who provided the French translation and Tamara Jones who aided in the drafting for this project, are all thanked.

Ed Hanna is thanked for providing comparative information on Red-shouldered Hawks in Ontario.

Financial assistance for this study provided by a Canadian Wildlife Service Grant to D. Bird and a Montreal Anglers and Hunters Inc. Award to the author are gratefully acknowledged.

List of Figures

Part I		Page
Fig. 1.	A map locating the main study area, in the hardwood forests in the northwest corner of the Vaudreuil County (VC).	4
Fig. 2.	Histogram of the numbers of each general prey type delivered to 8 Red-shouldered Hawk nests in 1979-1980.	10
Part II		
Fig. 1.	A map locating the main study area, in the hardwood forests in the northwest corner of the Vaudreuil County (VC).	35
Fig. 2.	Regression analysis of bill length (y axis) vs. age (x axis) for broods of 1 and 3.	39
Fig. 3.	Regression analysis of tarsus length (y axis) vs age (x axis) for broods of 1 and 3.	40
Fig. 4.	Regression analysis of tail length (y axis) vs. age (x axis) for broods of 1 and 3.	41
Fig. 5.	Regression analysis of wing length (y axis) vs. age (x axis) for broods of 1 and 3.	42
Fig. 6.	Regression analysis of weight (y axis) vs. age (x axis) for broods of 1 and 3.	43

List of Tables

Part I		Page
Table 1	Initial and final brood sizes in Red-shouldered Hawk nests in southwestern Quebec in 1979 and 1980.	6
Table 2	Percentage of prey items brought to Red-shouldered Hawk nests in 1979 and 1980.	11
Table 3	Meteorological data for the study area during May and June, 1979 and 1980.	12
Table 4	Percentage of the different prey types occurring in Red-shouldered Hawk pellets in 1979 and 1980.	14
Table 5	Weight of prey delivered to nestling Red-shouldered Hawks of small and large broods during 4-hour observation blocks.	15
Table 6	Frequency of prey deliveries to different brood sizes of Red-shouldered Hawks in 1980.	16
Part II		
Table 1	Initial and final brood sizes of Red-shouldered Hawks in southwestern Quebec in 1980.	36

List of Appendices

Part I		Page
Appendix I	A list of prey species brought to 8 Red-shouldered Hawk nests during 1979 and 1980.	29
Appendix II	A data sheet used for recording feeding activity of Red-shouldered Hawks.	30

PART I

Dietary Composition and Frequencies of Prey Delivery in Red-shouldered Hawk (*Buteo lineatus*) Broods in Southwestern Quebec.

1. Introduction

The influence of brood size on the feeding behaviour of adult birds and/or the growth of their young has been documented for several avian groups including passerines (Lack 1954, Seel 1970, Cronmiller and Thompson 1980), seabirds (Norman and Gottsch 1969), and raptors (Snyder and Snyder 1973, McInvaille and Keith 1974, Stinson 1977). These studies involved either the recording of the adult feeding rates in relation to the number of young in naturally occurring broods or experimentally removing or adding young to a nest and subsequently observing their growth and survival. Such work stemmed from classical studies by Lack (1954, 1966) who hypothesized that the number of young for which parent birds can provide food is limited. Accordingly, young of a brood above such a limit tend to be undernourished, resulting in a reduction in the reproductive fitness of these parents. Such a prediction is supported only if nestlings of larger broods receive less food than smaller broods and if fewer nestlings reach reproductive maturity. The ability of adult birds to supply food for different brood sizes (as reflected by growth rates and mortalities) varies among species (Askenmo 1977), necessitating separate studies of each species behaviour.

In his theory of "maximum reproduction" Lack (1954, 1966) emphasized that birds have evolved a clutch or brood size producing the greatest number of young. In broods of larger than optimal size, nestlings are usually poorly nourished and fewer young survive. An alternate theory termed "adjusted reproduction" (Skutch 1967)

stipulated that the reproductive rate is adjusted to the average annual mortality. However, according to Welty (1975), this theory may be most applicable to tropical species in more stable environments. Therefore, the northern Red-shouldered Hawk of the temperate region (Godfrey 1966) should support Lack's (1954, 1966) hypothesis.

The objectives of this part of the study were to determine the diet of the Red-shouldered Hawk (Buteo lineatus lineatus) in southwestern Quebec and to measure the effect of brood size on the frequency of feeding by the parents.

A number of specific predictions were made in this study with respect to Lack's hypothesis. First there should be a higher frequency of prey items brought to larger broods than smaller broods if adults are responding to the number of young in the nest, or the weight of prey brought to larger broods may be greater than for smaller broods. Perhaps a combination of the above may exist to compensate for the number of young in the nest. Second, the average amount of food in grams received by each member of a large brood may not be proportionate to that received by members of a small brood.

2. Study Area

Eight Red-shouldered Hawk nests were located in southwestern Quebec (Fig. 1) near the northern limit of their breeding range (Godfrey 1966). The study area consisted of approximately 200 Km^2 in the northwest corner of Vaudreuil County (45 15'N, 74 26'W),

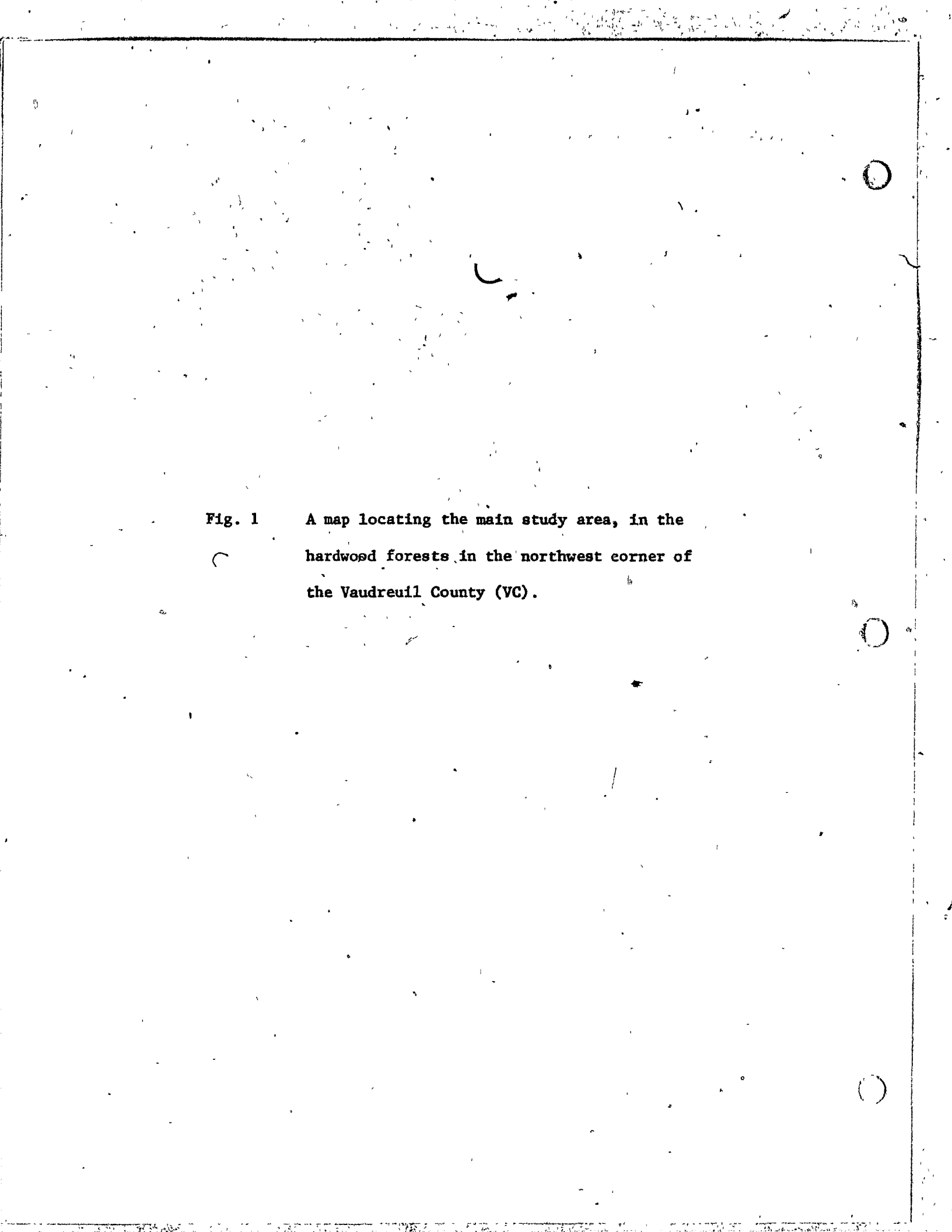
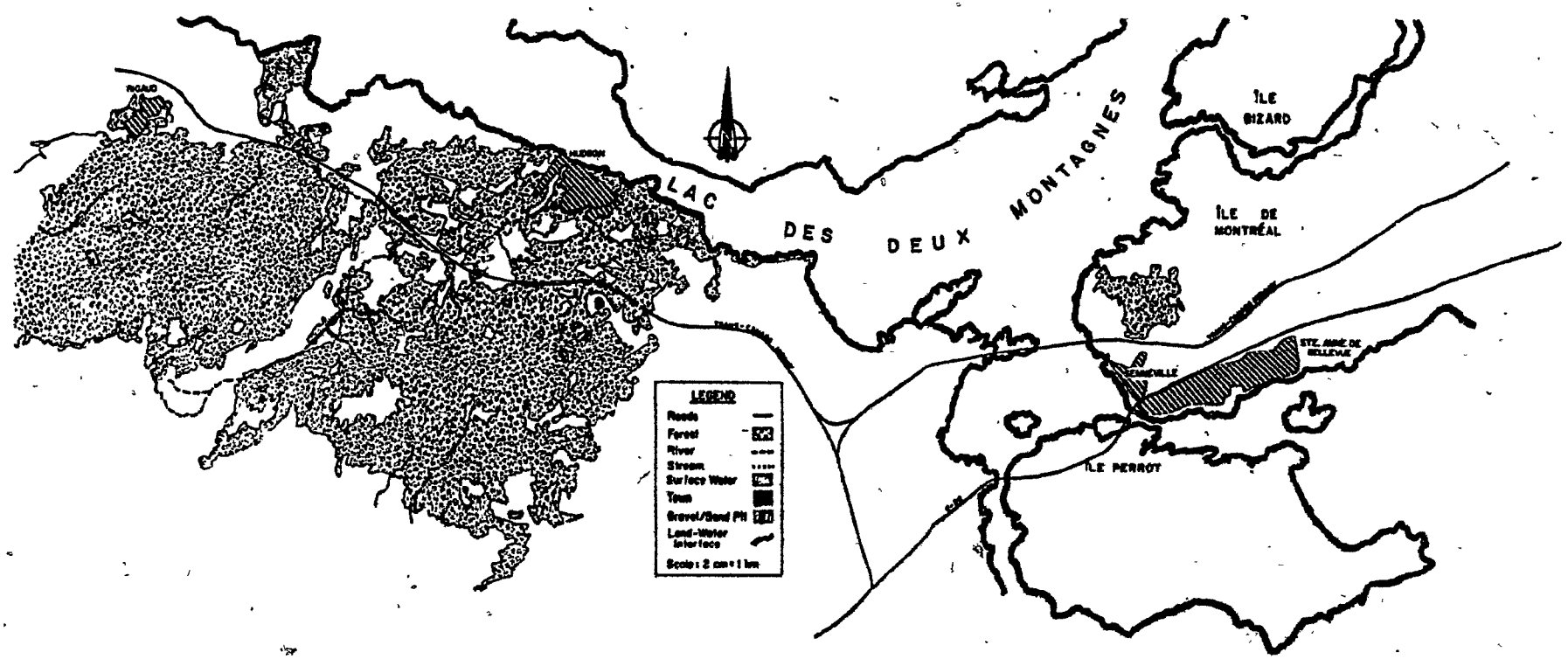


Fig. 1 A map locating the main study area, in the hardwood forests in the northwest corner of the Vaudreuil County (VC).


LAC DES DEUX MONTAGNES
ÎLE BIZARD
ÎLE DE MONTRÉAL
ÎLE PERROT
STE. ANNE DE BELLEVUE
SENNEVILLE
LEGEND
Roads
Forest
River
Stream
Surface Water
Town
Gravel/Sand Pit
Land-Water Interface
Scale : 2 cm = 1 km

about 45 km southwest of Montreal.

Newstrom (1978), Morris (1980) and Morris et al. (1982) have previously described this region in detail. The major tree species consisted of mature stands of Sugar Maple (Acer saccharum) and Beech (Fagus grandifolia), as well as Yellow Birch (Betula alleghaniensis), White Ash (Fraxinus americana), Basswood (Tilia americana), Largetooth Aspen (Populus grandidentata), Red Maple (A. rubrum) and Oaks (Quercus spp.).

3. Materials and Methods

In the spring of 1979 and 1980, Red-shouldered Hawk territories occupied in previous years were searched for active nests before complete foliation. New nests were located by seeking out vocalizations and observing displays of territorial adults.

A total of 8 nests were selected for observations of adult and nestling behaviour; 3 in 1979 and 5 in 1980. Local nest names and their initial and final brood sizes are indicated in Table 1. In 1980, 1 nestling was transferred during the very early nestling stage to another brood not under observation to create a range of brood sizes (2 - 4 inclusive, before mortalities).

A few days after hatching, wood and canvas observation blinds were constructed on the ground, usually on an upgrade, 20 - 30 metres away from the nest tree and equipped with a 20 - 45X spotting scope.

Information on the nestling diet (Appendix I) was collected during 400 hours of randomized observations made between 0800 and

Table 1 Initial and final brood sizes in Red-shouldered Hawk nests in south-western Quebec in 1979 and 1980.

Year	Local name of nest	Initial[1] brood size	Final[2] brood size
1979	Grahams	3	2
1979	Radisson	3	2
1979	Trans Canada	3	3
1980	Snowmobile	3	1[3]
1980	Seguin	3	1
1980	Old Fief	3	1
1980	Golf Course	4	3
1980	Trans Canada	3	3

[1] based on observations made within a few days of hatching or sooner.

[2] based on observations made close to fledging date.

[3] 1 young was transferred to another nest not included in the study.

1700 hours, beginning in mid-May and continuing through until the young left the nest, at the end of June. The behaviour of the adults and nestlings and general meteorological conditions during the observation periods were recorded on standard data sheets (Appendix II).

The mean weight of each mammalian prey type was calculated using the weights of tagged specimens from the Technical Services Branch of the National Museum of Natural History in Ottawa and the Redpath Museum at McGill University. The mean weights for frogs (except Rana sylvatica) and snakes were calculated from sampling efforts in the study area in 1979. All other weights of prey types were taken from Craighead and Craighead (1956).

Supplementary dietary information was determined from pellets within nests and around the base of nest trees. Pellets were air or oven dried, dissected with forceps and the occurrence of bone, scale, feather or insect remains were noted. Representative hairs (present in most pellets) were teased from the bulk of the pellet, and impressions of these were made in a polyvinyl acetate (Monsanto, Montreal) (Mathiak 1938; Williamson 1951). Scales on individual hairs are quite distinct in the various mammalian groups and can be identified with the aid of a reference collection and hair identification guides (Adorjan and Kolenosky 1969, Moore et al. 1974).

3.1 Data Analysis

Chi-square (1 and 2 sample) tests were used to analyse the general diet composition, between years, as well as the frequencies of prey delivery among the various brood sizes. A Kruskal-Wallis test was used to detect differences in the weight of prey among 1980 brood sizes. Differences in the individual weight of prey of small and large broods and differences in the total weight of prey delivered to nests during 4-hour observation blocks, were analysed using a two-tailed Mann-Whitney U Test. The latter test was also applied to daily rainfall and temperature data for the nesting periods to determine any significant differences in these two weather parameters between study years. A Spearman Rank Correlation Coefficient tested for any association between the total weight of the prey delivered per 4-hour block and the frequency of prey delivery in both small and large broods. The level of significance for the statistical tests was $p < 0.05$ unless stated otherwise. All statistical tests employed were described previously by Siegel (1956).

4. Results

4.1 General Diet

The general diet composition of the Red-shouldered Hawk nestlings, derived from observations at 8 nests in the 2-year study reflected a wide variety of prey species (Appendix I), predominantly small mammals and herpetofauna (Fig. 2).

Significantly more mammals ($X^2 = 4.54$, df = 1, $p<0.05$) than non-mammals were delivered to nests in 1980 as compared with 1979 (Table 2).

Chipmunks (Tamias striatus), shrews, moles, voles, and various species of mice composed the majority of mammalian prey (Appendix I) brought to the nests. Their relative proportions in the diet varied between years.

No significant difference was found in the amount of rainfall (Mann-Whitney U Test, $z = -0.359$, $p>0.05$) or temperature (Mann-Whitney U Test, $z = 0.626$, $p>0.05$) (Table 3) between the two study seasons and thus did not appear to contribute to the differences observed in the diet.

Interestingly, the occurrence of mammals to non-mammals in the pellets did not differ significantly between years (Table 4) ($X^2 = 1.0$, df = 1, $p>0.05$).

4.2 Prey Size and Frequency of Prey Delivery

When the mean weights of prey delivered per hour were plotted against the days of the nestling period in 1980 with each brood identified individually, values from broods of 1 and 2 more naturally grouped together as did values from broods of 3 and 4. Therefore it seemed reasonable to refer to broods of 1 and 2 as small broods and those of 3 and 4 as large broods.

The total weight of prey delivered in the 4-hour observation blocks was negatively correlated with the number of prey deliveries in both small (Spearmans Coefficient $r_s = -0.9501$, df = 27, $p<0.001$)

Fig. 2. Histogram of the numbers of each general prey type delivered to 8 Red-shouldered Hawk nests in 1979-1980.

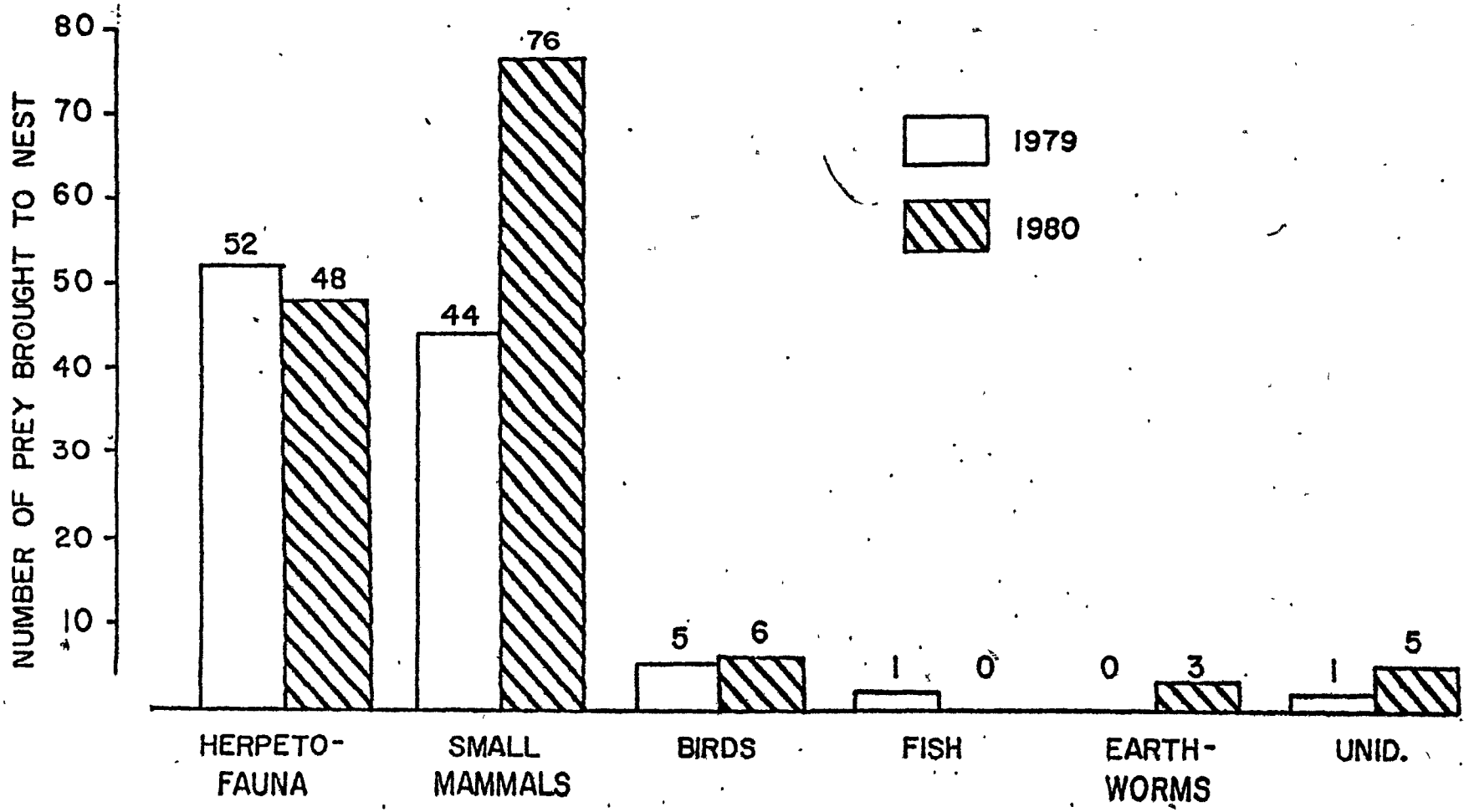

NUMBER OF PREY BROUGHT TO NEST
80
70
60
50
40
30
20
10
52
48
44
76
5
6
1
0
0
3
1
5
1979
1980
HERPETO-FAUNA
SMALL MAMMALS
BIRDS
FISH
EARTH-WORMS
UNID.

Table 2 Percentage of prey items brought to Red-shouldered Hawk nests in 1979 and 1980.

Taxonomic group	1979	1980	combined
mammals	42.7	55.1	49.8
herpetofauna	50.5	34.8	41.5
birds	4.8	4.3	4.6
fish	1.0	-	0.4
invertebrates	-	2.2	1.2
unidentified	1.0	3.6	2.5

Table 3 Meteorological data for the study area during May and June, 1979 and 1980[1].

1979	May	June	combined	1980	May	June	combined
mean precip. mm	86.1	39.1	62.6		44.8	36.2	40.5
mean temp. C°	13.7	18.6	16.2		13.2	17.4	15.3
mean range of temp. C°	8.3-19.1	12.6-24.5	10.5-21.8		6.8-19.6	11.7-23.0	9.3-21.3

[1]data from Rigaud meteorological station.

and large (Spearmans Coefficient $r_s = -0.7110$, df = 23, $p < 0.001$) broods (Table 5).

In 1980, the weight of prey delivered varied significantly among the different brood sizes (Kruskal-Wallis Test, H = 11.91, df = 3, $p < 0.01$) (Table 5). The total weight of prey brought to large broods during the 4-hour observation blocks was greater than that brought to small ones (Mann-Whitney U Test, z = -4.1114, $p < 0.05$). More specifically, the individual weights of prey items delivered to large broods were significantly greater than those brought to small broods (Mann-Whitney U Test, z = -4.5592, $p < 0.05$). This was not apparent in the smaller sample size of 1979 (Mann-Whitney U Test, z = -0.0334, $p > 0.05$).

The frequencies of prey delivery made during 4-hour observation periods among broods of different size in 1980 (Table 6) were significantly different ($X^2 = 19.13$, df = 3, $p < 0.001$). The number of prey delivered to broods of 3 was greater, but not significantly, than that delivered to broods of 2 in 1979 ($X^2 = 1.80$, df = 1, $p > 0.05$). Significantly more prey items were brought to large broods as compared to small broods (Table 6) ($X^2 = 15.82$, df = 1, $p < 0.001$).

Comparing maximum and minimum brood sizes in 1980, individuals of a brood of 4 did not appear to receive proportionately as much food as broods of 1. The total weight of prey brought to a brood of 1 was compared to that delivered to a brood of 4 during 7 randomly selected observation blocks (representing one sample observation week). The observed ratio was not the 1:4 ratio

Table 4 Percentage of the different prey types occurring in Red-shouldered Hawk pellets in 1979 and 1980.

Taxonomic group	1979[a]	1980[b]	combined
total mammals	68.4	64.1	65.8
bird feathers	10.0	18.8	15.4
insects	8.4	11.6	10.3
others[c]	13.2	5.5	8.5

[a] based on 110 pellets

[b] based on 163 pellets

[c] snake scales, fish scales

Table 5 Weight of prey delivered to nestling Red-shouldered Hawks of small and large broods during 4-hour observation blocks.

	Small			Large		
Brood size	1	2	combined broods of 1 and 2	3	4	combined broods of 3 and 4
Mean total prey weight ± s.e.m.*	41.76 ±7.78	22.66 ±5.51	37.81 ±6.398	182.29 ±50.60	88.5 ±21.68	152.96 ±35.86
Number of observation blocks	23	6	29	17	8	25

* standard error of the mean

Table 6 Frequency of prey deliveries to different brood sizes of Red-shouldered Hawks in 1980.

Brood sizes	Small 1	Small 2	Large 3	Large 4
Total number of prey brought to nests	38	14	64	22
Number of observation blocks *	24	6	17	8
Mean number of prey items delivered per block	1.6	2.3 (1.16)[a]	3.8 (1.25)[a]	2.8 (0.69)[a]

* one block = 4 hours $X^2 = 19.13$, df = 3, $p < 0.001$.

[a] mean number of prey items delivered per bird per block

expected, but 1:2.5 (275g:650g). The mean total weight of prey delivered per nestling during 23 observation blocks at 3 nests with a single nestling was 41.76 ± 7.78 grams.

This figure was more than quadrupled in the more common brood size of 3, where the average weight of prey delivered to nestlings was 182.29 ± 50.6 grams.

5. Discussion

5.1 General Diet

5.1.1 Observations

Since prey availability was not determined on a systematic basis during this study, one must assume that prey delivered to the young by adults and that identified in the pellets manifests part of a functional response by these raptors, i.e. the prey these hawks were utilizing reflects at least to a certain degree what was available in their habitat. This assumption was supported by another study in central Alberta (McInvaille and Keith 1974) where Red-tailed Hawks (Buteo jamaicensis) responded functionally to increasing hare populations.

The Red-shouldered Hawk is not considered to be a dietary specialist (Hausmann 1948, Stewart 1949, Portnoy and Dodge 1979) (Appendix 1). In Iowa, this species was able to adapt to changes in prey availability and successfully raise a brood on either mammalian or non-mammalian prey (Bednarz 1979). Information on

differences in the nutritional content between mammals and herpetofauna is not presently available, although food quality apparently can affect the growth rate of passerines under laboratory conditions (Berthold 1976), as well as the breeding strategy of Griffon Vultures, Gyps.spp. (Houston 1978).

Prey conspicuousness is enhanced by activity, increasing vulnerability to predation (Craighead and Craighead 1956). Animal activity in turn, can be affected by weather on a species-specific basis (Bider 1968; Stinson 1980). Although no significant difference was found in rainfall or temperature between the two study seasons, spring water levels for which data were not available may have influenced the availability of herpetofauna. In Iowa, Bednarz (1979) observed Red-shouldereds taking more amphibians in years of high water levels. The unusual lack of snowfall in the winter of 1979 in southwestern Quebec likely affected the water levels, as well as low temperatures may have reduced the amphibian and reptile prey base in the following spring. Sand-transect data from Lac Carre, Quebec (46° 09' N, 74° 29' W) demonstrated a drastic reduction in herpetofauna activity during the summer of 1980 (J.R. Bider, pers. comm.), possibly due to the harsh 1979 winter conditions.

Diet can change seasonally and geographically (Craighead and Craighead 1956, Herrera and Jaksic 1980, Picozzi 1980, Hanna unpubl. data) but in this study area, herpetofauna, specifically frogs appeared to be one of the predominant prey types throughout the nestling period. Nest observations and those of B. Lyon (pers. comm.) in 1976 at Mt. St.-Bruno, Quebec, as well as the sampling

efforts near nest sites in 1979, indicate that Wood Frogs (Rana sylvatica), Green Frogs (Rana clamitans) and Leopard Frogs (Rana pipiens) were the most frequently delivered prey items. Craighead and Craighead (1956) reported similar findings in Michigan.

The combination of small mammals and herpetofauna accounted for more than 85% of the total diet in either year.

The eastern chipmunk was an important mammalian prey species for Red-shouldered Hawks in the study area, especially in 1979. It was also a dominant prey item for this species in Massachusetts (Portnoy and Dodge 1979) and western Maryland (Janik 1980) as well as for the Cooper's Hawk (Accipiter cooperii) and the Broad-winged Hawk (Buteo platypterus) in the latter locality. Portnoy (1974), Janik (1980) and Morris (1980) all suggested the reproductive cycle of Red-shouldered Hawks roughly coincided with the emergence of young chipmunks in late May and early June (Smith and Smith 1972, Pidduck and Falls 1973). The earliest observation of a chipmunk being delivered to a nest in either year was the first week in June.

5.1.2 Pellet Analysis

Osseous material usually does not survive the digestive processes of Buteos well enough for positive identification in pellet analysis (Errington 1930) because Falconiforme gastric juices are highly acidic (Duke et al. 1975). This could have accounted for the absence of soft amphibian bones in Red-shouldered Hawk pellets as considerable amounts of herpetofauna were included

in the diet. Similar findings were reported for Red-shouldereds by Portnoy (1974) and Snyder and Wiley (1976). The only herpetofauna remains that do persist are reptile scales composed of keratin (Patt and Patt 1969), a fibrous protein relatively acid-insoluble (Lehninger 1970). The presence of more avian remains in pellets of 1980 than in 1979 does not coincide with nest observations. Perhaps the prolonged oven drying of pellets in 1980 before dissection dessicated the brittle feathers and disintegrated the pellets. As a result, partial pellets were sometimes counted as whole pellets, biasing the occurrence of bird remains upwards.

5.2 Prey Size and Frequency of Prey Delivery

The negative correlation observed between the total weight of prey delivered during an observation period and the frequency of prey delivery in both large and small broods implies that adult Red-shouldered Hawks made fewer trips when a greater total weight of prey was delivered. The feeding rates for a number of raptor species show a similar trend (Newton 1979). In broods where adults were able to meet the prey demands of their young, frequencies of prey delivery were lower with larger prey sizes. It may be more profitable for parents to deliver both large and small prey when hunting near the nest, but to bring only large prey when hunting far from the nest because of the time and energy used to fly back and forth (Newton 1979).

The general increase in the frequency of prey delivery to larger broods has also been recorded for Great Tits (Parus major)

(Gibb 1955) and Grey Catbirds (Dumetella carolinensis) (Johnson and Best 1982). Also, female Red-winged Blackbirds (Agelaius phoeniceus) raising experimentally large broods made significantly more feeding trips to their nests than did females of pooled natural and control nests (Cronmiller and Thompson 1980). Experimental addition and removal of young to broods of Cooper's Hawks by Snyder and Snyder (1973) demonstrated that adults showed no hesitation in feeding extra young. Their large broods were generally, but not consistently, fed more often than smaller ones, but this was attributed to differences in habitat quality. Without considerable manipulation of brood size and concurrent monitoring of prey populations or activity, it cannot be disproved that the results may have been due to habitat quality differences at different nests, and/or between the 2 study years. Some constancy of habitat quality seems apparent between nests as prey was not superabundant at any nest in either year, i.e. stock-piling of prey in the nests was never observed. Only 1 pair of adult Red-shouldereds in both years was able to successfully rear all members of its brood, possibly indicative of poor habitat quality. Since southwestern Quebec is near the northern limit of the breeding range for this species (Godfrey 1966), geographical location may be important in determining habitat quality and influencing the productivity for this particular population.

Results on the influence of brood size on food quantities eaten by nestlings have varied, both inter- and intra-specifically (Newton 1979). In nests of Sharp-shinned Hawks (Accipiter striatus),

Cooper's Hawks and Sparrowhawks (Accipiter nisus), the amount of food consumption was not dependent on the number of young. In contrast, the amount of food consumption was dependent on brood size for Ospreys (Pandion haliaetus), Marsh Harriers (Circus aeruginosus), Kestrels (Falco tinnunculus) and Peregrines (Falco peregrinus) (Newton 1979).

In this study of Red-shouldered Hawks, the amount of food consumption was generally greater in larger broods. This species may also be compensating for the number of nestlings by delivering prey of a greater weight to larger as compared to smaller broods. In Orkney, Scotland feeding and delivery rates of prey items at nests of Marsh Harriers were low, but regardless of brood size, this was apparently compensated for by many items being large (Picozzi 1980). Red-tailed Hawks in Alberta brought 73% more prey in terms of biomass to broods of 2 compared to broods of 1 (McInvaille and Keith 1974). At 1 of 2 nests of Cooper's Hawks studied, where experimental shifting of nestlings raised the brood size from 2 to 5 young, the average weight of prey delivered per day showed a corresponding increase (Snyder and Snyder 1973). Parent Grey Catbirds fed larger broods more frequently, but did not increase the volume of food delivered per feeding trip, leading Johnson and Best (1982) to conclude that the food requirements per nestling actually decreased as the brood size increased. Although Red-shouldered Hawk nestlings of the maximum brood size of 4 in this study did not receive proportionately as much food as those of a brood of 1, each nestling of the more

common brood size of 3 (initially 7 of 8 broods in this study) was provided with considerably more food than a nestling from a brood of 1. This implies a limitation to the number of young parent birds can provide food for, similar to Lack's (1954, 1966) findings for some passerine species. The inability of parent birds to increase the amount of food in proportion to the number of young in nest by increasing the frequency of delivery and/or selection of larger food items, has been documented for a number of species. These include various African Swallows, Hirundinidae and Swifts, Apodidae (Moreau 1947), Starlings (Starnus vulgaris) (Kluijver 1933), Robins (Turdus migratorius) (Lack and Silva 1949), Great Tits (Gibb 1955), Field Sparrows (Spizella pusilla) (Best 1977), Eastern Bluebirds (Salia salis) (Pinkowski 1978), Purple Martins (Progne subis) (Walsh 1978), Red-tailed Hawks (McInvaille and Keith 1974) and perhaps Cooper's Hawks (Snyder and Snyder 1973).

6. Conclusions

The diet composition of Red-shouldered Hawks in the Hudson-Rigaud area of southwestern Quebec showed that herpetofauna and small mammals were predominant prey types. The annual variation of the 2 major prey types over the 2 years may be related to winter weather conditions prior to each nesting season. In 1980, parents of both large and small broods tended to bring fewer prey items when the total weight of prey delivered in an observation block was greater. Broods of 3 were delivered prey more frequently and prey of an average greater weight than that brought

to broods of 1. Nestlings of the largest brood size (4) in the study area were not fed proportionately as much as nestlings of the smallest brood. This may be interpreted to support Lack's (1954) hypothesis and similar studies of feeding behaviour in other bird species.

To thoroughly determine reproductive fitness in relation to brood size however, we must await results of long-term studies on the growth and mortality in different brood sizes, the effect of age and experience on the hunting abilities of the adults, the importance of habitat and prey quality, and the influence of sibling aggression on nestling survival in this species.

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Appendix I

Common name	Scientific name	year observed as prey species 1979	1980
Wood frog	Rana sylvatica	x	x
Leopard frog	Rana pipiens	x	x
Green frog	Rana clamitans	x	x
Eastern chipmunk	Tamias striatus	x	x
Meadow vole	Microtus pennsylvanicus	x	x
Boreal redback vole	Clethrionomys gapperi	x	
Mice	Peromyscus spp.	x	x
Eastern garter snake	Thamnophis sirtalis sirtalis	x	x
Red-bellied snake	Storeria occipitomaculata	x	
Yellow shafted flicker	Colaptes auratus	x	
Black throated blue warbler	Dendroica caerulescens		x
Starnose mole	Condylura cristata	x	x
Hairytail mole	Parascalops breweri	x	x
Shorttail shrew	Blarina brevicauda	x	x
Smaller shrews	Sorex spp.	x	x
Meadow jumping mouse	Zapus hudsonicus	x	x
Woodland jumping mouse	Napaeozarpus insignis	x	x
Eastern grey squirrel	Sciurus carolinensis	x	x
Norway rat	Rattus norvegicus		x
Unknown fish sp.		x	
Red-spotted newt	Notophthalmus viridescens	x	

Appendix II

FEEDING ACTIVITY

DATE:

NEST:

OBSERVER:

OBSERVATION PERIOD	start	finish
time		
total hours		
temperature °C		
wind direction		
wind speed		
cloud cover		
precipitation		
total precip.		

SETTING: start | finish

prey description	prey size	time prey brought in	time prey removed	prey ripped apart by adult	prey fed to young	young feed themselves	eating by adult	food stealing amongst young	start/end of feeding bout

COMMENTS:

PART II

The Relationship of Brood Size to Parental Care and Growth of Nestling Red-shouldered Hawks (*Buteo lineatus*) in Southwestern Quebec.

1. Introduction

Relatively little quantitative information exists specifically on the growth of raptors (Olendorff 1974, Parker 1976, Stinson 1977, Moss 1979, Bird and Laguë 1982). The effect of brood size on growth of non-raptorial avian species has been extensively studied, although, interspecific results are highly variable (Askenmo 1977). This demands that each species be examined individually with respect to the effects of brood size.

Generally, Prince and Ricketts (1981) noted that the growth of nestling seabirds was determined by the energy of parent birds and the rate of supply of nutrients, including 3 major components: food size, feeding frequency and food quality. Ricklefs (1968) originally claimed that the general avian growth rate (based on weight) was probably independent of nutrition, unless starvation was extreme. More recently, Ricklefs et al. (1980) reported that in altricial and semi-altricial species such as raptors, growth may be limited by the feeding rate. Other environmental factors affecting growth are habitat quality (Hagen 1969), temperature (Brookes and May 1972; Ross 1980) and brood size (Askenmo 1973, 1977). Genetic factors must also be important in determining the rate of growth, but quantitative studies are scanty (Garnett 1981).

The aim of this study was to quantify some aspects of the growth of nestling Red-shouldered Hawks (Buteo lineatus lineatus) in Southwestern Quebec. The effect of brood size on the growth of selected body parameters, as well as on the nest attendance by the adults in the form of the amount of time spent brooding and the

frequency of delivery of greenery to the nest were examined.

Penak and Bird (M.S. in prep) showed that Red-shouldered Hawk broods of 3 were fed more frequently and were delivered prey of a greater weight than that brought to a brood of 1. Since the amount of food intake may affect the growth of birds of prey (Ricklefs et al. 1980) it was predicted that Red-shouldered young from broods of 3 would grow more quickly than those without siblings.

A larger number of nestlings in a brood generally reduces the surface-volume ratio and consequently the heat loss (Hamas 1981). Based on this, it was predicted that the amount of time adults spent brooding would be less for nests with 3 young as opposed to those with 1 young.

Finally, in some passerines it is known that a greater amount of nesting material increases the insulative properties of a nest (Skowron and Kern 1980). Since the need for more insulation (which reduces heat loss) would be less for larger broods than smaller ones, it was predicted that the delivery of greenery to the nest should be greater in broods of 1 compared to broods of 3.

2. Study Areas

Growth data were collected from young at 9 Red-shouldered Hawk nests located in 2 areas in southwestern Quebec (Fig. 1). The main study area contained 8 of these 9 nests and was described in more detail by Penak and Bird (M.S. in prep.).

The ninth nest was located in the demonstration forest ($2.0 km^2$) of the Morgan Arboretum (45^{o} 57'N, 74^{o} 26'W), Macdonald Campus of

McGill University (Fig. 1) located approximately 30 km east of the main study area. As part of the Upper St. Lawrence section of the Great Lakes-St. Lawrence Forest Region (Rowe 1972), the dominant tree associations are similar to those described for the main study area (Part I of this thesis).

3. Materials and Methods

A total of 9 Red-shouldered Hawk nests (Table 1) were visited in 1980 every 4 to 7 days during May and June to weigh and measure the young. In order to create a larger range of brood sizes, 1 nest was manipulated. This involved the removal of 1 nestling from a brood of 3 and transferring it to another brood of 3 (Table 1). Mortalities occurred at all nests except 1 and only growth data of surviving chicks were analysed. The brood size used in analyses was that which existed for at least half (17 days) of the nesting period.

Chicks were lowered in a drawstring bag to the ground where body parameters were measured. Nestlings were not measured on rainy or cold overcast days to avoid possible hypothermia.

Approximate hatching dates were determined by observations made either directly after climbing the nest tree or adjacent tree, or indirectly from the ground with the aid of a spotting scope. Estimates of chick age were accurate to about ± 2 days. Weights at hatching were determined from 2 nestlings, each from different nests. Chicks were weighed individually with Pesola spring scales.

Since all nests could not be visited before the first feeding

Fig. 1 A map locating the main study area, in the hardwood forests in the northwest corner of the Vaudreuil County (VC).

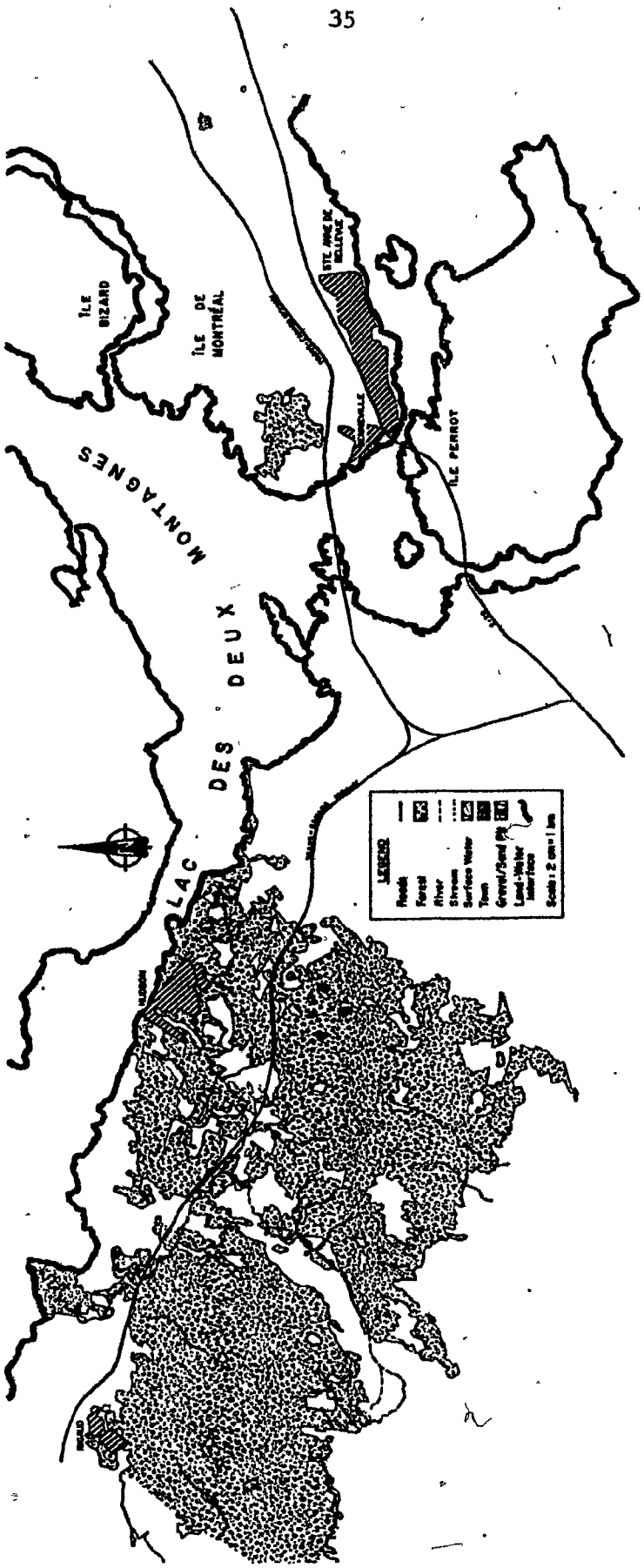

ÎLE BIZARD
ÎLE DE MONTRÉAL
STE. ANNE DE BELLEVUE
ÎLE PERROT
MONTAGNES
LAC DES DEUX
LÉGENDE

Table I Initial and final brood sizes of Red-shouldered Hawks in southwestern Quebec in 1980.

Year	Local name of nest	Initial brood size[1]	Manipulation[2]	Final brood size[3]
1980	Golf Course	4	0	3
1980	Arboretum	4	0	3
1980	Snowmobile	3	-1	1
1980	Bedard	3	+1	2
1980	Deserted Barn	3	0	1
1980	Gravel Pit	3	0	1
1980	Old Fief	3	0	1
1980	Trans Canada	3	0	3
1980	Seguin	3	0	1

[1] based on observations made within a few days after hatching or sooner.

[2] indicates if a young was added (+) or removed (-) from a nest, or not manipulated (0).

[3] based on observations closest to fledging date.

of the day, crop fullness was determined visually as either 1/4, 1/2, 3/4 or completely full. The weight of a full crop was measured in a laboratory specimen (post mortem) and the total body weight of each of the individuals in the nest was adjusted for crop fullness, where applicable. It was assumed that the crop represents a constant percentage of body weight throughout development (G. Duke, pers. comm.).

The following linear measurements were taken on the right side of the body, measured to the nearest 0.01 mm with vernier calipers or a wooden ruler: bill length, tarsus length, the first 2 secondary wing feathers and the two central retrices length. Bill length was measured including the cere. All other growth parameters were measured as described by Baldwin et al.(1931) and Olendorff (1972).

Red-shouldered nestlings could not be reliably sexed on the basis of weight or the various measurements, as there is some overlap of these growth parameters (J. Mosher pers. comm.).

3.1 Data Analysis

Step-wise multiple regression analysis with some polynomial terms was performed to determine and contrast patterns of growth. A new variable was created to account for any interaction of brood size and age. Computer programs employed were those of the Statistical Analysis System (Barr et al. 1976) and the Statistical Package for the Social Sciences (Nie et al. 1975). Chi-square 1-sample tests (Siegel 1956) were used to analyse the frequency of brooding and the delivery of greenery to the nests by the adults.

Tests were performed at the 0.05 level of significance unless indicated otherwise.

4. Results

The nesting chronology of Red-shouldered Hawks began later and hatchlings seemed somewhat larger (40 grams, n = 2) in southwestern Quebec than those in western Maryland (27 grams, n = 1) (Janik 1980). Young Red-shouldered Hawks left the nest at approximately 35 days of age. On the last nest visit, the average weight of a fledgling was 533.5 grams, representing a 12-fold increase over the mean hatching weight.

Multiple regression analysis demonstrated that the growth of bill (Fig. 2, $F = 168.9$; 3, 85 d.f.), tarsus (Fig. 3, $F = 900.95$; 3, 85 d.f.), and tail feather (Fig. 4, $F = 4.32$; 3, 53 d.f.) were significantly different in broods of 3 and 1. The growth of wing feathers (Fig. 5) and weight gain (Fig. 6) were not significantly different.

Generally nest attendance was greater in large broods (with 3 young) as compared to small broods (with 1 young). The amount of time spent brooding by parents with 3 young (13.25 minutes per 4-hour observation block) was significantly greater than that spent by parents with only a single young (7.82 minutes per 4-hour observation block) ($X^2 = 31.9$, df = 1, $p<0.001$).

The frequency of delivery of greenery to nests with 3 young (16 observations during 17 observation blocks) was significantly greater than that of nests with 1 young (2 observations during

Figures 2 - 6 inclusive are the Regression analyses for growth of body parameters where Y = body parameter, X_1 = age and X_2 = brood size. Triangles represent growth data points for broods of 1 and squares represent growth data points for broods of 3. Regression lines are represented by a solid line for a brood of 3 and a broken line for a brood of 1.

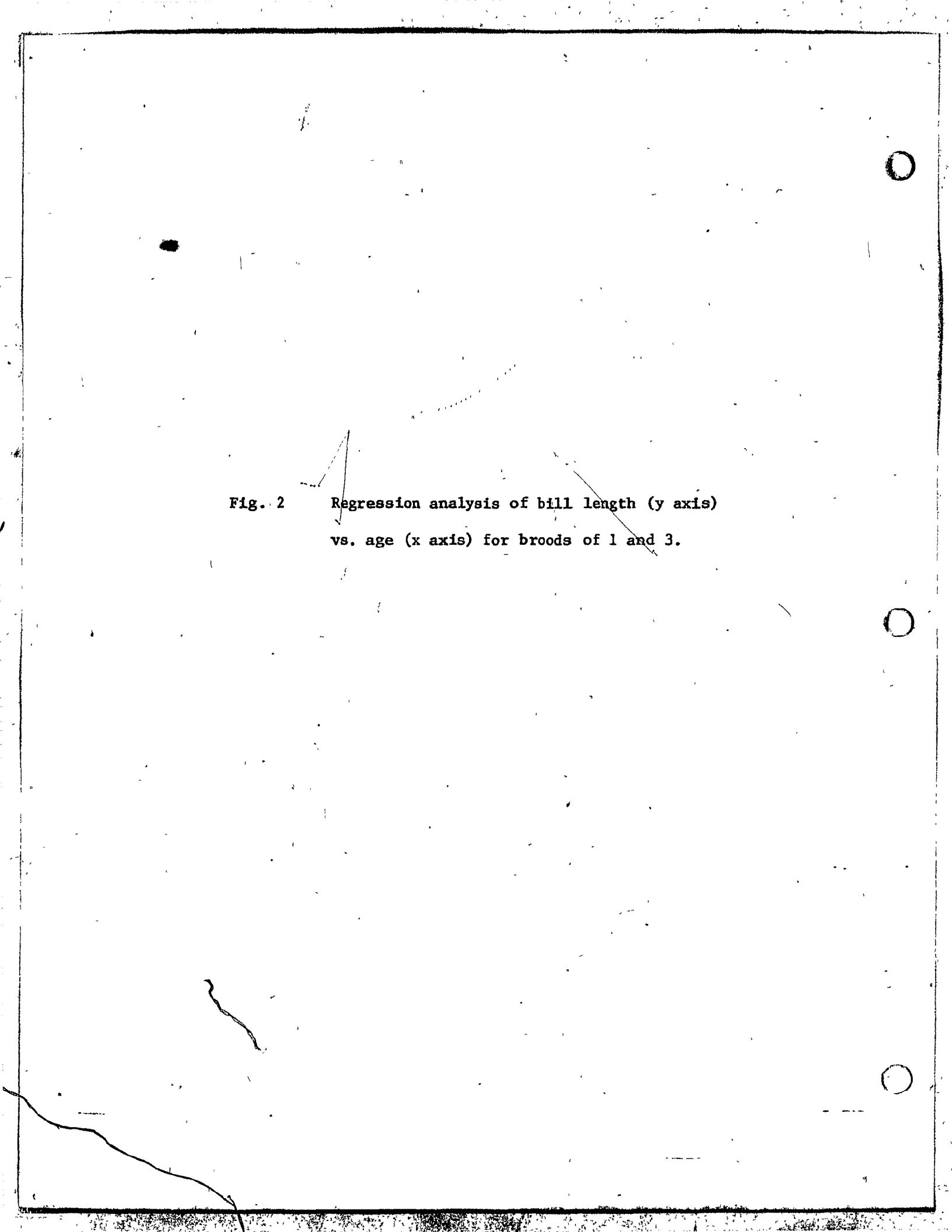


Fig. 2 Regression analysis of bill length (y axis) vs. age (x axis) for broods of 1 and 3.

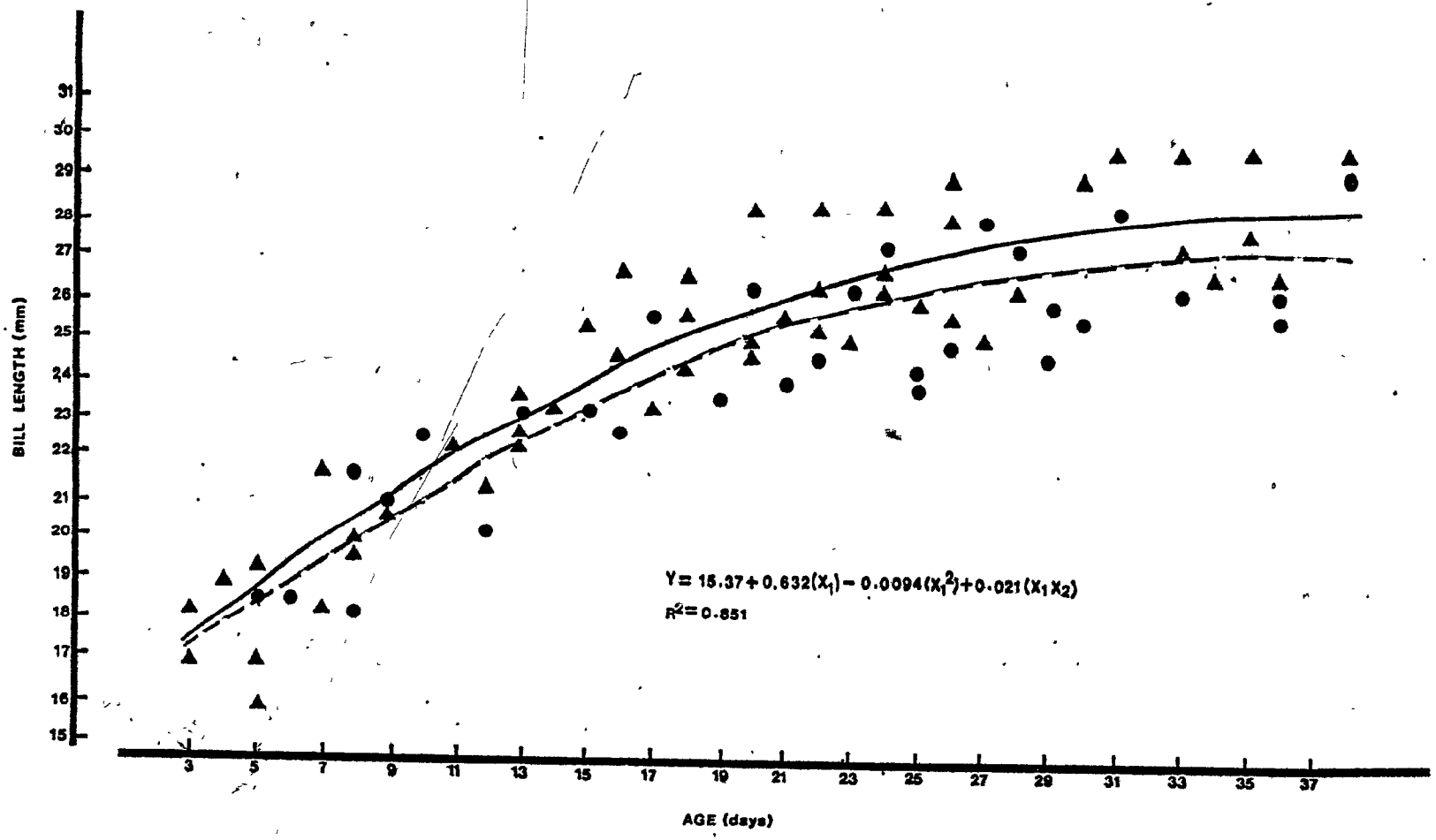

BILL LENGTH (mm)
31
30
29
28
27
26
25
24
23
22
21
20
19
18
17
16
15
3
5
7
9
11
13
15
17
19
21
23
25
27
29
31
33
35
37
AGE (days)
Y= 15.37+0.632(X1)−0.0094(X1²)+0.021(X1X2)
R²=0.851

Fig. 3 Regression analysis of tarsus length (y axis) vs. age (x axis) for broods of 1 and 3.

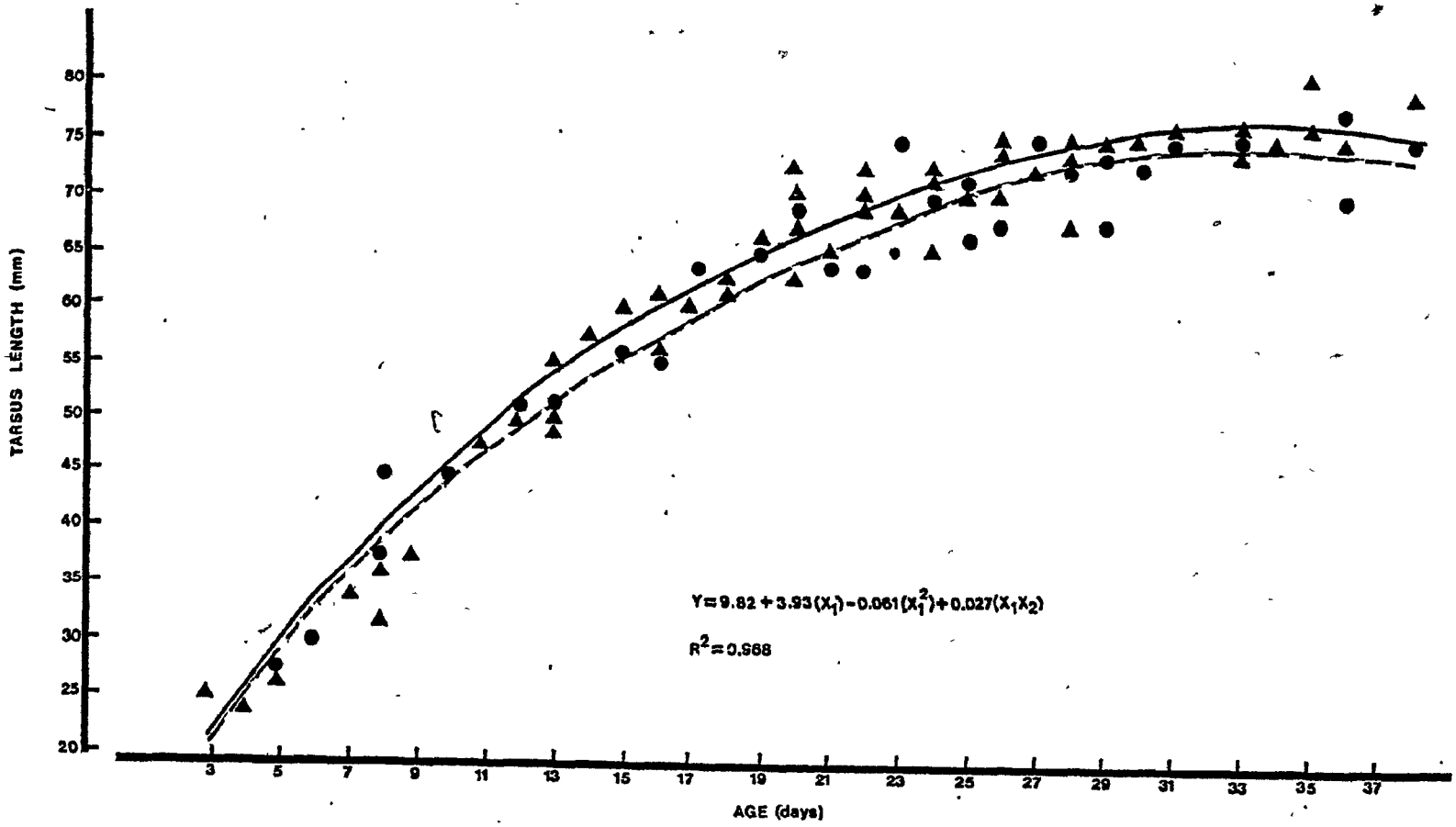
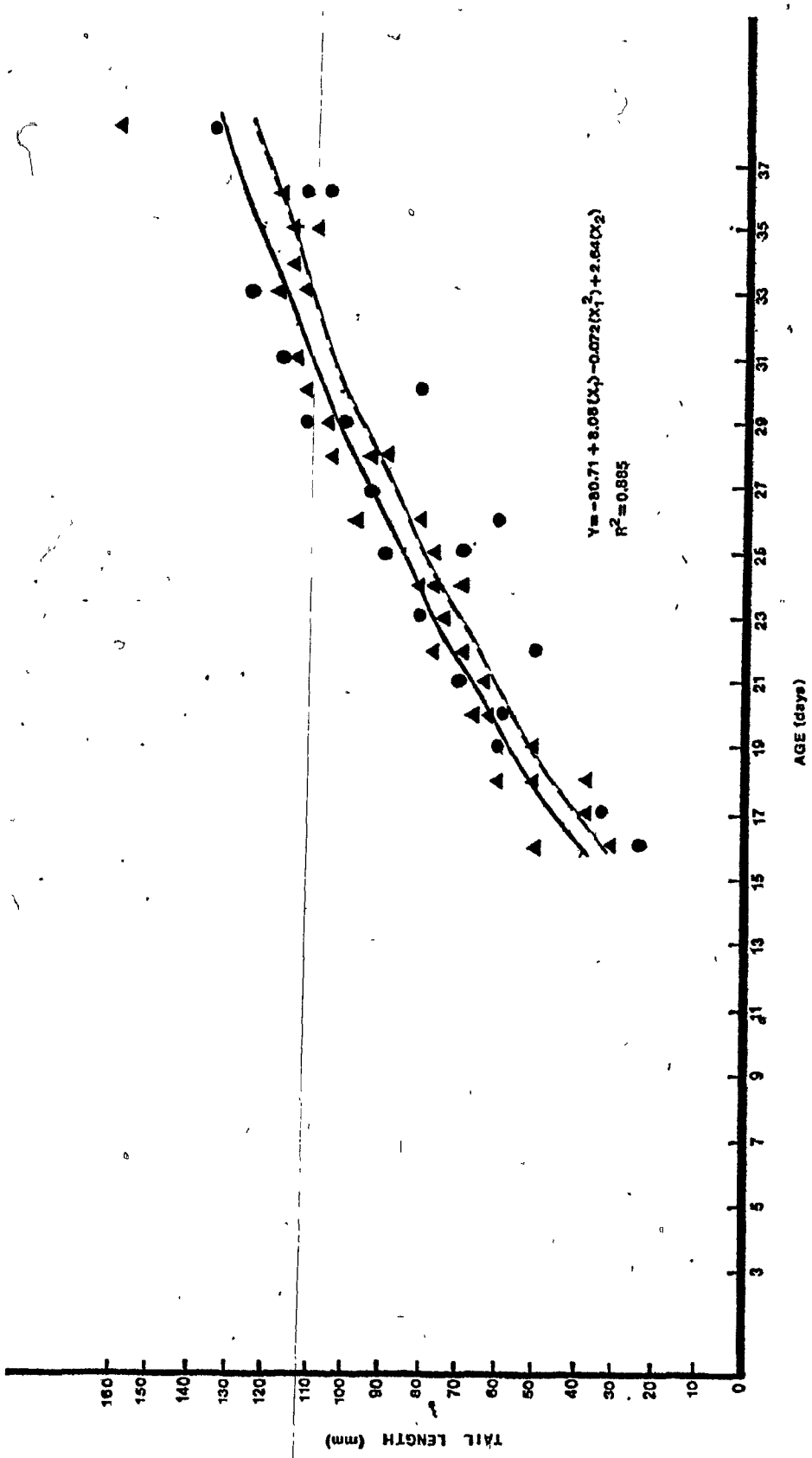

TARSUS LENGTH (mm)
80
75
70
65
60
55
50
45
40
35
30
25
20
3
5
7
9
11
13
15
17
19
21
23
25
27
29
31
33
35
37
AGE (days)
Y=9.82+3.93(X1)-0.061(X1²)+0.027(X1X2)
R²=0.968

Fig. 4 Regression analysis of tail length (y axis) vs. age (x axis) for broods of 1 and 3.


TAIL LENGTH (mm)
AGE (days)
Y = -80.71 + 8.08(X1) - 0.072(X1²) + 2.64(X2)
R² = 0.885

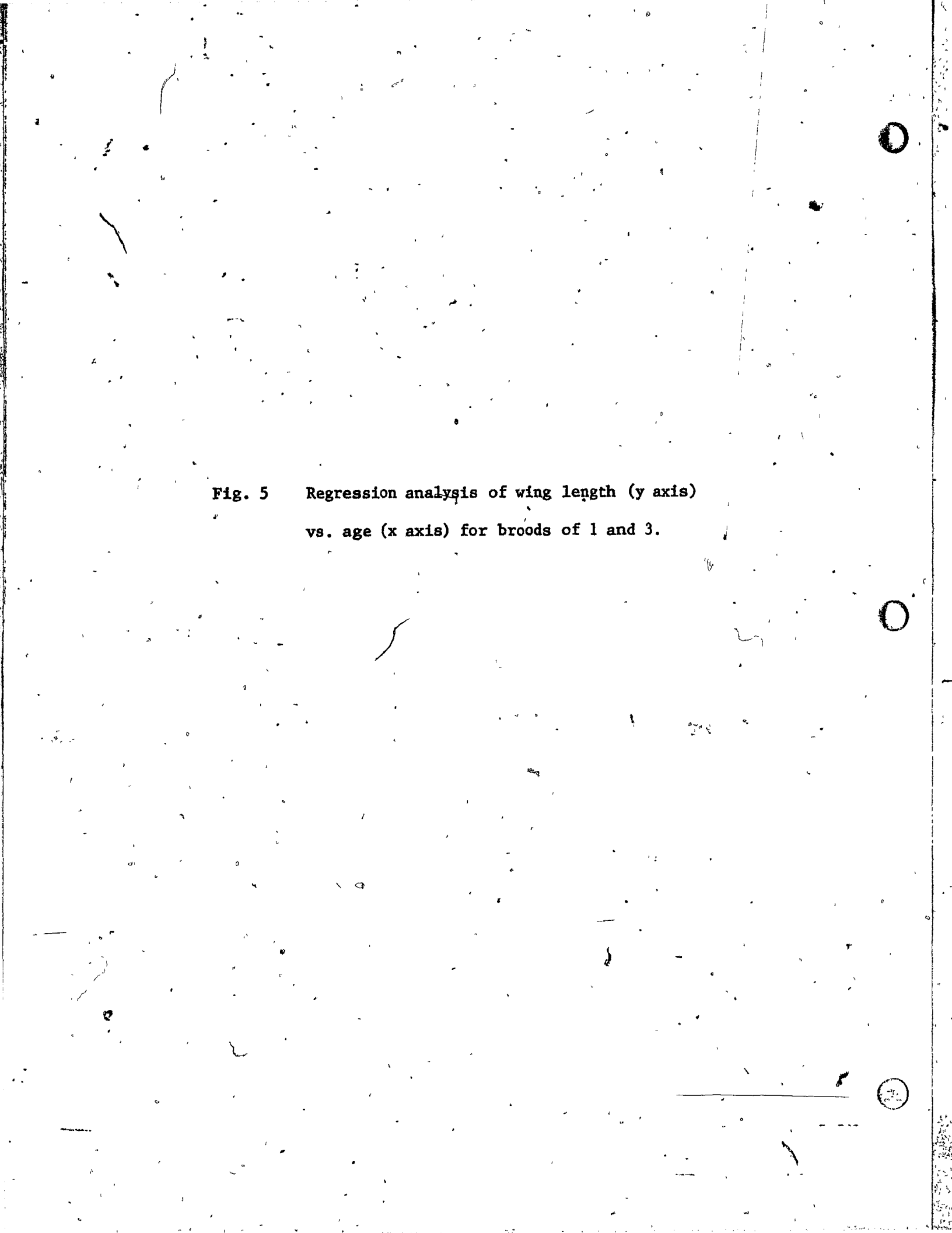


Fig. 5 Regression analysis of wing length (y axis) vs. age (x axis) for broods of 1 and 3.

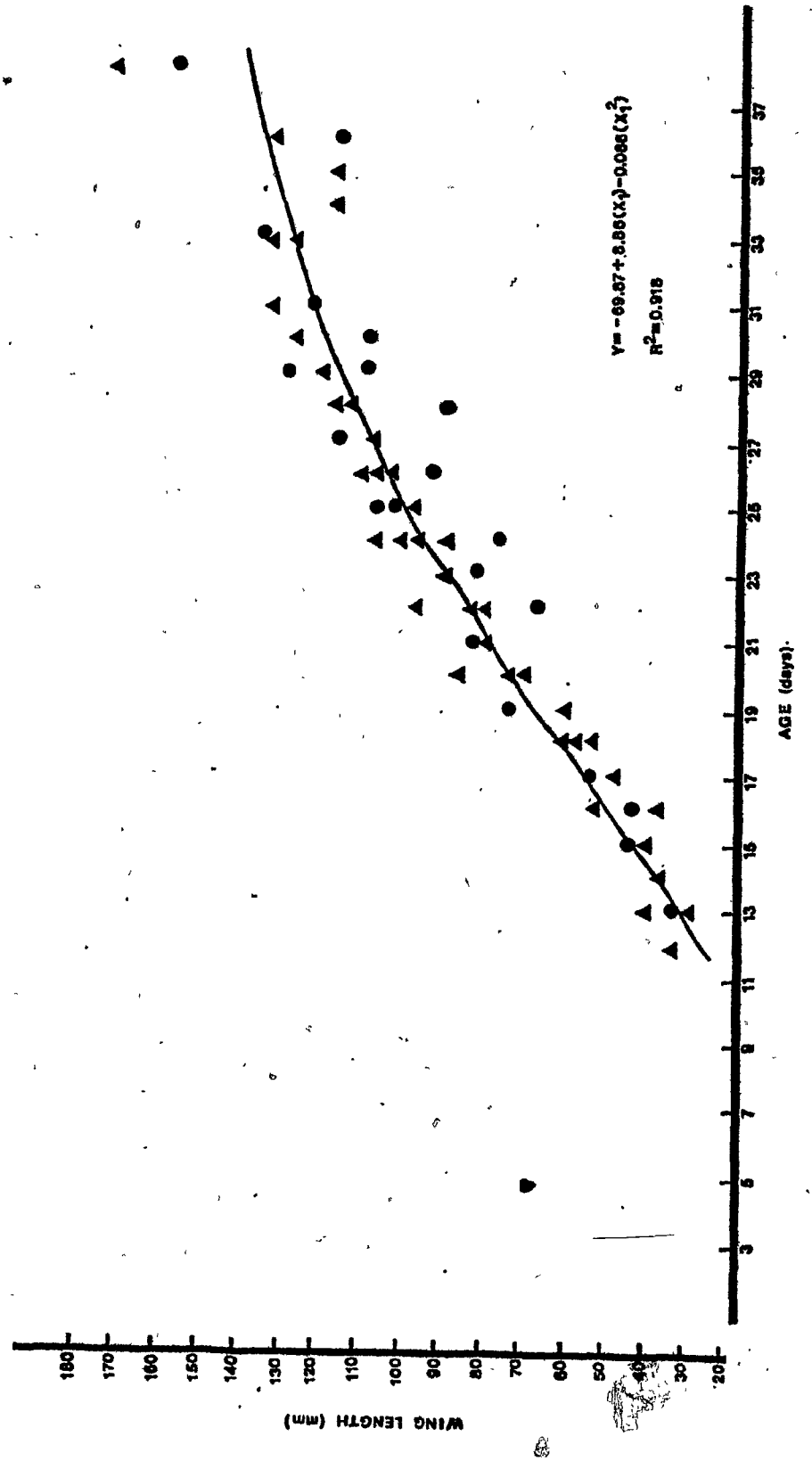
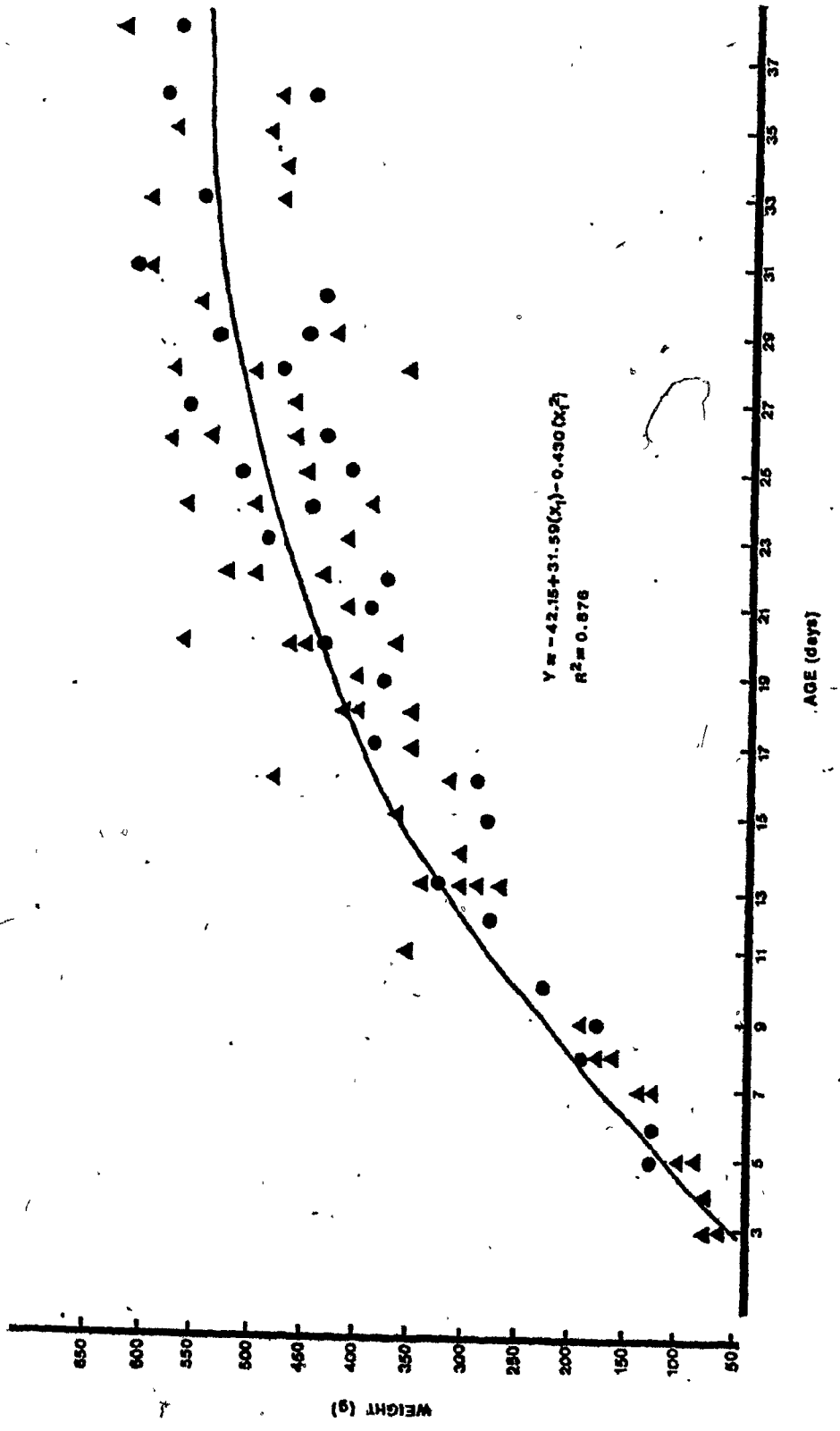

Y= -69.87+8.86(X1)-0.066(X1²)
R²=0.918
AGE (days).
WING LENGTH (mm)

Fig. 6 Regression analysis for weight (y axis) vs age (x axis) for broods of 1 and 3.


WEIGHT (g)
650
600
550
500
450
400
350
300
250
200
150
100
50
AGE (days)
3
5
7
9
11
13
15
17
19
21
23
25
27
29
31
33
35
37
Y = -42.15+31.59(x1)-0.430(x1²)
R²= 0.876

24 observation blocks) ($X^2 = 16.68$, df = 1, $p < 0.05$).

5. Discussion

Growth curves for most of the body parameters of Red-shouldered Hawks measured were generally sigmoid in shape as described by Sumner (1929, 1933) and Moss (1979) for other raptorial species. However, wing and especially tail feather measurements were truncated at both ends, thereby creating a more linear-shaped graph similar to that found for the growth of the tarsus and primary feathers of Sparrowhawks (Accipiter nisus) (Moss 1979).

The weight curves for Red-shouldereds were more variable than those for feather or bone development. This was also observed in Sparrowhawks (Moss 1979) and Hen Harriers (Circus cyaneus) (Picozzi 1980) particularly when food was not plentiful.

In Red-shouldered Hawks, the rate of growth of bill and tarsus length were greater in broods of 3 compared to broods of 1. Although this has not been previously documented for any raptor species, the growth of selected body parameters of Ipswich Sparrows (Passerculus sandwichensis) (Ross 1980) and Willow Warblers (Phylloscopus trochilus) (Tiainen 1978) showed a similar pattern.

The tail feather length for broods of 3 was significantly larger than that for broods of 1. Significant differences found between broods for bill and tarsus length were a result of an interaction between brood and age, whereas brood size alone accounted for the difference in tail feather length between the two brood sizes.

The increased food supply delivered to larger broods of Red-shouldered Hawks (Penak and Bird, ms. in prep.) and corresponding greater growth in such broods supports the claim that growth in semi-altricial species may be limited by feeding rate (Ricklefs et al. 1980).

Studies on the effects of brood size on the growth of different raptor species have shown inconsistent results, similar to those of passerine studies (Askenmo 1977). Growth rate was found to be independent of brood size in both Sparrowhawks (Accipiter nisus) (Newton 1978, Moss 1979) and American Kestrels (Falco sparverius) (Balgooyen 1976). However, an inverse relationship existed between brood size and fledging weight of Ospreys (Pandion haliaetus) (Stinson 1977).

Since the amount of brooding by Red-shouldered Hawks was greater in broods of 3 compared to broods of 1 (not as originally predicted), larger broods were probably kept warmer than small ones. The thermoregulatory advantages of a large brood should allow parents more time to forage (Dunn 1976) and permit nestlings to expend less energy to keep warm (Mertens 1969), but at least the former was not observed in this study. The time spent brooding by parents was related to brood size in Grey Catbirds (Dumetella carolinensis) (Johnson and Best 1982), but not Purple Martins (Progne subis) (Walsh 1978).

Broods of 3 also had more greenery delivered to the nest than broods of 1, contrary to the original prediction. Although the delivery of greenery to raptor nests is a common practice, its function is still obscure (Olendorff 1974). One proposed function

is that it provides insulation (Brown and Amadon 1968). Skowron and Kern (1980) noted in songbirds that nests with greater insulation values are those with the least light penetration. The greenery added to the inside of Red-shouldered Hawk nests may have decreased light penetration and increased the insulative properties.

Ross (1980) suggested that nutritional as well as thermal factors may affect growth rate. This may also be the case for the growth of Red-shouldered Hawks in southwestern Quebec.

6. Conclusions

The relative contributions of 1) the increased food supply by the parents, 2) the increased warmth associated with more siblings in the nest, 3) more brooding by the parents, 4) the addition of more greenery to the nest or 5) a combination of these factors to the greater growth observed in broods of 3 compared to broods of 1 remain to be resolved. Carefully controlled experimentation isolating one factor at a time should provide more insight into this problem.

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