A METHOD FOR APPRAISAL OF ANNUAL REPRODUCTIVE SUCCESS IN THE BLACK BRANT POPULATION

A

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A METHOD FOR APPRAISAL OF ANNUAL REPRODUCTIVE SUCCESS IN THE BLACK BRANT POPULATION

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ABSTRACT

A technique for appraisal of reproductive success in the black brant *Branta bernicla orientalis* Tougarinov population is presented. The system uses plumage characteristics distinguishing juvenile birds from others. The entire population gathers in Izembek Lagoon, Alaska in fall where the technique was developed. Annual reproductive success in brant varies widely, but management has not varied accordingly.

A large stand of eelgrass furnishes food for brant while in the Lagoon, and affects opportunities for observing them. This, and physical limitations on travel within the Lagoon prevent random data collection, hence the statistical validity of inferences drawn from the data was examined, revealing one source of bias. The most efficient data gathering period proved to be the first half of October. An unsuccessful experiment using marked birds in a change-in-ratio estimator is reported.

A hypothetical population was developed on the basis of the highest reproductive success observed. This was fitted into a mathematical model of three variables: (1) age distribution in the population, (2) age specific recruitment rates, (3) age specific mortality rates. Simulation with the model showed the effects of these variables in an increase or decline of the population.

Management should be designed to allow an increasing population, which requires regulations based on recruitment.

PREFACE

This study emerged from my employment position as Refuge Manager of the Izembek National Wildlife Range. It addresses management needs of a race of geese, the black brant, concentrated in a rather small population in the Pacific and Arctic Oceans where in its migrational orbit it visits four countries. This population gathers in fall in Izembek Lagoon, Alaska and migrates *en masse* to the Pacific coast of Mexico in early November, about four-fifths going no further than the lagoons of Baja California. Later, when they return north in spring the birds follow the coast of the U. S. and Canada before striking west across the Gulf of Alaska once again to Izembek Lagoon. The Lagoon provides the staging area for a quick flight to the nesting grounds in Canada, Alaska, and the Soviet Union.

The hope, of course, is that part or all of this work may be pressed into service in the interests of perpetuation of this population. That hope is based on the assumption that the factors affecting mortality are knowable and manageable within the framework of wildlife management today. Unfortunately, this seems unlikely to remain a valid assumption. The discovery of large reserves of petroleum on Alaska's north coast has created a demand to transport the oil by pipeline across the State to a deep-water port at Valdez, and thence by immense ships along coastal Canada and the U. S. to distant ports. Much of it seems destined for the deep-water ports of Puget Sound.

Atlantic Richfield's new Cherry Point refinery, situated just south of the British Columbia border in Puget Sound lies in the heart of the staging area for northbound adult brant. Here the paired adults gather between late February and early May each spring on the northern migration. Both the U. S. and Canadian governments acknowledge that a major oil spill may be expected in the Puget Sound area when super-tankers transport crude oil from Valdez to the 11 refineries in the greater Puget Sound basin. Such an event occurring between February and May would threaten destruction to a large part of the reproducing segment in the black brant population, and the hosts of other water birds inhabiting the region. Official support for the pipeline and marine transport system from the U. S. Federal Government and that of the State of Alaska indicates that a decision to proceed will be based on economic considerations - not ecological ones.

I acknowledge the privilege of living and working on the Izembek National Wildlife Range, conferring as it did the opportunity and freedom to study this population of geese. This is my debt to the U. S. Fish and Wildlife

Service. The late Arthur S. Einarsen furnished encouragement in the early stages of this study. Both Dr. Calvin J. Lensink and Dr. Thomas W. Barry freely furnished their data, answers to my questions, and inspiration as the study unfolded. My professional colleagues on the Wildlife Range, Messrs. Jack B. Helvie, Palmer C. Sekora, and Edgar P. Bailey participated in collection of the data used in this study. The members of my graduate committee, Dr. David R. Klein, Dr. James C. Bartonek, Dr. C. Peter McRoy, and Dr. Samuel J. Harbo furnished guidance and helpful criticisms in the preparation of this manuscript. My wife, Dr. Dorothy M. Jones, who participated in much of the field work and in the generation of this manuscript, fanned the spark of endeavor into flame when it languished.

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INTRODUCTION

Isolation once conferred immunity from excessive hunter kill for the population of black brant *Branta bernicla orientalis* Tougarinov. Gregarious in disposition, the birds assemble in concentrations on nesting grounds, migration way-stops, and wintering areas in remote locations. But now with rapid transportation increasingly available for hunters, these very concentrations expose the species to heavy hunting mortality. Such circumstances emphasize the need for methods of population appraisal more responsive to change than is an annual winter inventory. Einarsen (1965:97) articulated the need for management of the species on a refined basis, and suggested, "that inventories dealing with total numbers are perhaps not as significant as an inventory of reproduction for each year."

The present management system for black brant is based on a winter inventory conducted in January and takes no account of reproductive success. Furthermore, it is dominated by the inertia of an established bag limit that has not been changed for several years despite the demonstrated variation in reproductive success. I am motivated in this study by a conviction that a total inventory in January is not enough. These pages are concerned with an inventory that is responsive to annual recruitment in the black brant population; and I offer a simulation model whereby the interactions of the parameters of age distribution, recruitment rates, and mortality rates may be analyzed.

European observers conducted appraisals of reproductive success in brent geese *Branta bernicla bernicla* (L.) by determining the proportion of juvenile birds in wintering flocks (Burton 1958). Recognition of distinctive plumage in the juveniles (birds less than a year old) formed the basis of the appraisal. In 1963 the Izembek National Wildlife Range instituted this type of appraisal as an annual procedure in which all professional employees participated as observers. The results of each year's appraisal constitute Einarsen's "inventory of reproductive success" and permit a closer inspection of his call for "management of the species on a refined basis."

In addition to the winter inventory, current management of the species depends upon hunting mortality estimates based on band returns and hunter questionnaires. Because of the confined wintering areas, and the nature of wintering brant to distribute themselves in small flocks which can be counted from an airplane, described in Leopold and Smith (1953), the winter inventories are regarded as among the most accurate available. On these two bases regulations are announced each fall to deal with hunting pressure, most of which will occur in February and March a full year after the inventory. Both Cooch (1963) and Barry (1962) emphasize the adverse effects of late seasons on reproductive success in Arctic nesting geese, and Lynch and Singleton (1964) confirm that these effects are measurable.

It is now appropriate to examine the implications of the three sets of information available concerning the population of black brant. These are (1) the winter inventory, (2) the published hunting mortality estimates, and (3) the Izembek appraisals of reproductive success. If the mortality estimates are reasonably correct it should be possible to estimate the size of the spring population by subtracting mortality from the population as inventoried in January. The reproductive growth in the population may then be calculated on the basis of the Izembek appraisals in the fall to yield an estimate of the population size at the time of the next inventory.

In January 1964 the winter inventory produced an estimate of 185,300 black brant in the continental population (Smith and Jensen 1970). According to the report of hunting mortality in the Waterfowl Status Report for 1965 (Hansen and Hudgins 1966:75) this population sustained a hunting loss of 5,100 birds before returning to the Arctic. No natural mortality rates have been developed for brant, but three are available for other geese. These are 5.6% for dusky Canada geese *Branta canadensis occidentalis* (Baird) (Henny 1967), 8.2% for snow geese *Chen hyperborea* (Pallas) (Rienecker 1965), and 10% for Canada geese *Branta canadensis* (L.) in New Zealand (Imber and Williams 1968). Application of any of these rates to the black brant population as inventoried in January 1964 requires the concession that natural mortality exceeds the reported hunting mortality. However, proceeding with the calculations, using the natural mortality rate for dusky Canada geese, the equation reads as follows.

185,300 - 5,100 (the reported kill) - 10,400 (natural mortality calculated at 5.6%) = 169,800

Thus approximately 170,000 birds found their way north in spring *if all the data are correct*. When in the fall of 1964 this population, together with young of the year, returned to Izembek Lagoon the appraisals demonstrated the presence of 27% first-year birds in the population (Table 1), a growth of approximately 63,000 birds to a total of about 233,000. The winter inventory of January 1965 produced a total of 165,700 (Smith and Jensen 1970).

In these calculations I have started with the January inventory date, and applied the reported hunting mortality plus natural mortality in the interval between the time of inventory and onset of nesting about June 1st.

Table 1. Mean Percentage of Juveniles Recorded in Each Subsample, the Mean for all Areas and its Standard Deviation (σ).

Year	Area "A" Percent Juveniles	Area "B" Percent Juveniles	Area "C" Percent Juveniles	Area "D" Percent Juveniles	Area "E" Percent Juveniles	Mean for all areas	σ
1963	-	-	18.1	28.3	-	23.8	7.262
1964	29.3	31.3	23.4	25.1	-	25.9	3.983
1965	35.9	17.8	18.6	26.3	19.5	21.6	7.975
1966	30.8	44.7	40.8	42.4	39.3	40.1	5.340
1967	30.0	16.4	17.8	16.6	16.1	17.5	6.330
1968	20.1	16.5	15.3	17.9	20.5	17.5	2.332
1969	40.6	18.7	27.6	-	26.9	26.1	9.449
1970	47.4	24.8	34.5	44.8	45.2	38.1	9.638

The reported hunting mortality does in fact cover this period, but it may be argued that natural mortality should be applied over a more extended period. At present any attempt to do so would be speculative, as indeed the choice of mortality rates applicable to the dusky Canada goose must be regarded. Later in this manuscript I introduce the concept of an anniversary date in applying mortality and recruitment rates, and for this the reader is directed to the section dealing with a hypothetical population. For the present my purpose is to demonstrate that the January inventory reflects mortality rates much higher than the estimates show.

Applying the same computations to the inventory of January 1965 yields much the same picture:

$$165{,}700 - 12{,}500 - 9{,}200 = 144{,}000.$$

Using the published figures of hunting mortality (Hansen 1967) and the natural mortality rate developed for the dusky Canada geese the population reaching the Arctic in 1965 would have numbered about 144,000. When the birds returned to Izembek Lagoon with 24% first-year birds (Table 1) the population should have numbered about 179,000. The winter inventory of January 1966 tallied 156,900 birds (Smith and Jensen 1970).

Using the same mortality rate and the published hunting mortality estimates (Martinson *et al* 1968) I calculated (computations not shown) the population returning to the Arctic in the spring of 1966 at about 139,000 birds. The youngsters produced by this population represented 40% (Table 1) of the total returning to Izembek Lagoon that fall, or about 93,000 for a grand total of approximately 232,000. The winter inventory reported 179,000. Note that the inventory is sufficiently responsive to indicate the bumper crop of young birds, but the disparity between the projected and the inventoried population is disturbing.

The estimates of wintering populations (Smith and Jensen 1970) from 1951 through 1970 vary about a mean of 141,713 with a standard deviation (hereinafter abbreviated by the Greek symbol σ) = 27,408. No definite pattern of increase or decline is discernable and a manager with no more information than the winter inventory and the published hunting mortality estimates would be entitled to regard present management as adequate. But the availability of an additional set of information which furnishes an estimate of total reproduction offers the manager a check on the balance between recruitment and mortality. The figures discussed above seem to indicate that mortality estimates are substantially lower than the real mortality. This must await further study, but in the meantime the means and the need for refined management is at hand.

The data accumulated for this study in eight years represent 161,085 observations of individual birds in 789 flocks varying in size from five birds to over 3,000. When the results from the first two years of effort showed that this appraisal method would really work, the question arose regarding its statistical validity. The size of the data set now available permits an examination to answer this question. Following an introduction to Izembek Lagoon and the field methods employed in the appraisal, I shall address this question (Section 1). When the statistical validity of the field methods is established I shall discuss conversion of the appraisal from an essentially research effort to a planned activity (Section 2). Finally, I shall present a hypothetical population deduced from the 1966 appraisals (Section 3), and a simulation model that facilitates analysis of the interactions of recruitment, mortality, and age structure in the population (Section 4).

Section 1.

STATISTICAL VALIDITY OF THE APPRAISAL

THE STUDY AREA

Izembek Lagoon, a shallow embayment of Bering Sea on the Alaska Peninsula, centers about Grant Point at 55° 16'N, 162° 53'W. An all weather road, legacy from World War II, leads to this point furnishing ready access to the Lagoon. Though McRoy (1966) has given a detailed account of the Lagoon, a fresh view is in order here. An observer standing on the promontory of Grant Point in, say, early October of any year, receives a visual and auditory impression of a massive gathering of geese. By this date in autumn all, or nearly all of the North American population of black brant lie within ten miles of that point, busily feeding on eelgrass *Zostera marina* L. Of all the manifold characteristics evident in Izembek Lagoon, none is more pervasive than the eelgrass. McRoy (1970:6) refers to the eelgrass in Izembek Lagoon "as the largest reported single stand," but this understates the case. The waters of the Lagoon run green with eelgrass by early October, and every biological entity in the Lagoon, including man, feels its influence. It dominates the geese. By October literally tons of eelgrass leaves are adrift in the Lagoon, impeding boat operations, coming ashore in vast windrows, and everywhere attracting the feeding geese.

Izembek Lagoon possesses a well-developed system of channels that have their heads in the eelgrass beds carpeting the tide flats. These drain seaward in sometimes meandering courses on the ebbing tide through three gateways to the Lagoon. At high water a boat may travel to anywhere in the Lagoon, but on the ebbing tide these channels furnish the only avenue of travel. At low water a boatman follows the channels easily as they then resemble rivers and creeks with bright green banks, but at intermediate stages both channels and shallows become invisible. Then the boatman finds his way with difficulty. Depths varying from two or three inches to several feet, and bottom sediments from sand and clam shells to stinking ooze, frequently halt the boat and grind the propellor to uselessness or force the boatman to wade. Such physical characteristics limit access to various parts of the Lagoon, especially distant ones at low or intermediate tide levels.

FIELD METHODS

The presence of white margins on the tips of scapulars, secondaries, and wing coverts distinguish first-year brant from all older classes (Kortright 1953). These distinctions remain until the first moult at the age of one year, and are clearly visible on a bird viewed at a range close enough to observe feather patterns. This fact formed the basis of appraisal methods adopted on the Izembek Range, and for this study.

In this manuscript the terms "first-year bird" and "juvenile" are used interchangeably, and refer to a brant in its first year of life. All older brant, including yearlings, wear generally the same plumage. Though yearlings (birds in their second year of life) can frequently be distinguished by minor plumage characteristics, I do not consider that this holds for all specimens hence in this manuscript they are listed as *in adult plumage*. Note the distinction between being in adult plumage and being adult. In this manuscript I use three divisions in terms of biological maturity: juveniles as the first age class, immatures as the second and third age classes, adults as the fourth and older age classes. But more about that later.

Using a good quality, tripod-mounted telescope as basic equipment, the Izembek observers inspected brant visually and recorded each bird observed as in juvenile or adult plumage. Tally counters, one in each hand, served to record observations. Under favorable weather and lighting conditions maximum effective range for the required observation was about 400 yards, but most data were gathered at much shorter ranges.

Concentrations of brant in Izembek Lagoon are not random. The location of eelgrass, whether rooted in beds or drifting with tide and wind, governs flock distributions.

The observer judged these factors, together with those of weather and visibility in deciding his observation post. The birds move toward the beach on a flooding tide and out when it ebbs, so the problem was to select a location where birds concentrate within range on the flooding tide.

Not many locations within the Lagoon satisfy both these conditions and the practical ones of time and effort required to reach the site at low tide levels. The desirability of choosing samples at random was always recognized, but every effort to disperse observation points without regard to flock distribution led to inadequate data, or more commonly none at all. To achieve the large samples considered necessary the observers gathered data in areas favored by the birds. Continuous flock movements led all observers to believe that constant exchange occurred, conferring randomness impossible to achieve through distribution of observation points.

The locations from which large samples have been collected are not precisely designated spots on some particular beach of the Lagoon; they are areas (Figure 1). An observer might have chosen one side of a protective mound in one set of weather conditions, and another a half mile down the beach in different weather. Flocks of brant tend to drift parallel to the beaches in one direction

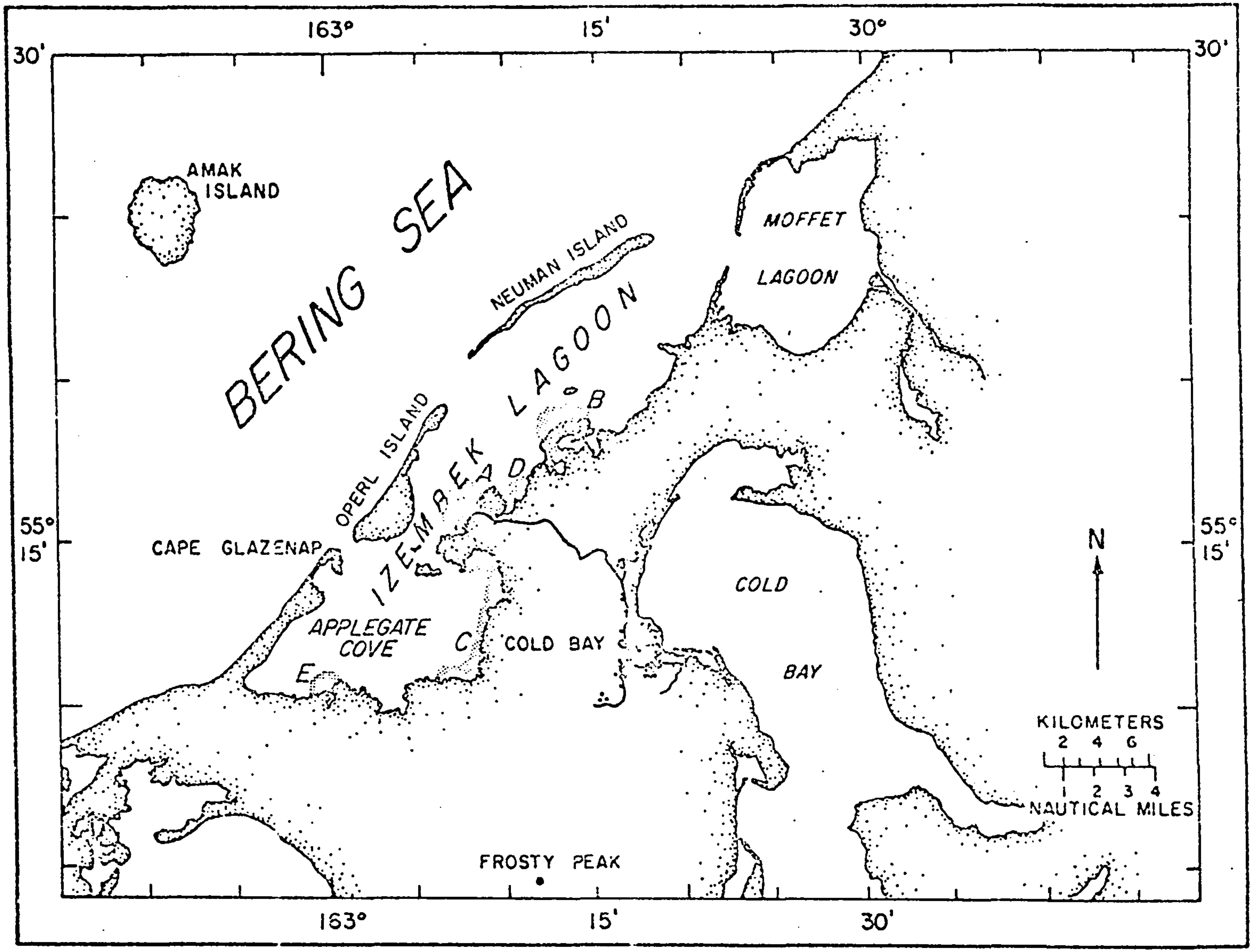

Fig. 1. Chart of Izembek Lagoon, Alaska showing locations of brant counts.

while feeding, so that the same birds could be observed from any of a number of locations along a strip of beach. Blinds were not necessary. The shores of the Lagoon possess rank vegetative cover, principally beach rye grass *Elymus arenarius mollis* Trin. ex Spreng., in which an observer takes cover, not so much to hide from the birds as to seek shelter from weather. The birds did not take alarm at an exposed observer, even though he moved a bit, so long as he did not stand upright. Bright yellow oilskins, regular items of apparel both in and out of boats in Izembek Lagoon did not deter approaching birds. This accords well with Hochbaum's (1955:26) description of "tolling" waterfowl with a plaid shirt. Disturbing factors, in addition to waterfowl hunters already mentioned, include airplanes and avian predators. Bald eagles *Haliaeetus leucocephalus* (L.) constitute the most potent disturbing factor of all. They are common in the region, and the approach of one puts all species of geese to flight.

VALIDITY OF APPRAISAL METHODS

In this section I shall apply statistical methods to assess the possibility of sorting in the population according to (1) area of sampling, (2) flock size, and (3) the two halves of the fall period. This section will conclude with a discussion of an experiment involving marked birds.

The basic data, consisting of the total count of each flock and the number of juveniles in each, appear in Appendix I. Appendix II presents these same data as totals. They fall, in this presentation, into five divisions annually which I have designated areas "A" through "E" on the basis of the locations from which the counts originated. I wish to emphasize that these are areas (Figure 1). In this manuscript I refer to these five divisions of the annual sample as subsamples. Though a small number of observations have been compiled on the Wildlife Range in the lagoons of Morzhovoi Bay they are not included in this study.

The statistical analyses are based on the frequency of juveniles in the counts; not as flocks, but as totals of flocks in the various categories tested. In each case this is reduced to the proportion of juveniles expressed as a percentage of the total in the appropriate category.

VALIDITY ACCORDING TO AREA OF SAMPLING

The mean percent juveniles in the annual samples varied from 17.5 to 40.1 in the eight years, reflecting variations in reproductive success. The five area subsamples varied about the annual mean with a standard deviation from 2.332 to 9.638. Table 1 shows these data.

A total of 161,085 observations comprise the eight annual samples. Of this total 26.8% were juveniles. The five subsamples varied from 23% juveniles to 37% with a standard deviation from the percent juveniles in the total of 5.740. The scale of the contribution from each subsample to the total varied from 13% to 30%, reflecting the difficulties of securing counts regularly from some areas. These data are shown in Table 2. The extreme deviation of the area "A" subsample (+10.2) indicates sorting at this location.

To pursue this indication of sorting further I have assembled a contingency table using all the area subsamples for all years 1964 through 1970 (Table 3). In this and all other statistical manipulations in the manuscript I have employed the formulations of Bailey (1964). The figures in the contingency table are from Table 1; the expected value (in brackets) is the mean percent juveniles in the total sample for the appropriate year, while the observed value (entered in the table above the expected value in each cell) is the percent juveniles in the subsample. Testing the hypothesis that there is no sorting of the black brant population in Izembek Lagoon I calculated the value of χ^2 (chi square), and entered the value at the bottom of each cell. The test showed significant sorting at the 0.05 significance level in the contributions from area "A".

Table 2. The Cumulative Contribution of the Five Subsamples to a Total of 161,085 Observations Recorded in Izembek Lagoon, 1963 - 1970.

Area	Percent contribution to total sample	Percent juveniles in subsample total	Deviation from percent juveniles in total sample
"A"	16	37	+10.2
"B"	28	23	- 3.8
"C"	30	24	- 2.8
"D"	14	26	- 0.8
"E"	13	29	+ 2.2
Percent juveniles in total sample = 26.8			σ = 5.740

Table 3. Calculation of χ^2 (Chi Square) Using all Area Subsamples and all Years Beginning with 1964. Observed Percentage Juveniles in Top of Cell, Expected Percentage in Brackets, Contribution to χ^2 in Bottom of Cell.

Area	1964	1965	1966	1967	1968	1969	1970	Totals
	29.3	35.9	30.8	30.0	20.1	40.6	47.4	
"A"	[25.9]	[21.6]	[40.1]	[17.5]	[17.5]	[26.1]	[38.1]	
	.446	9.467	2.156	8.928	.386	8.055	2.290	31.708
	31.3	17.8	44.7	16.4	16.5	18.7	24.8	
"B"	[25.9]	[21.6]	[40.1]	[17.5]	[17.5]	[26.1]	[38.1]	
	1.125	.668	.527	.069	.057	2.098	4.642	9.186
	23.4	18.6	40.8	17.8	15.3	27.6	34.5	
"C"	[25.9]	[21.6]	[40.1]	[17.5]	[17.5]	[26.1]	[38.1]	
	.241	.416	.012	.005	.276	.086	.240	1.376
	25.1	26.3	42.4	16.6	17.9		44.8	
"D"	[25.9]	[21.6]	[40.1]	[17.5]	[17.5]		[38.1]	
	.024	1.022	.131	.046	.009		1.178	2.410
		19.5	39.3	16.1	20.5	26.9	45.2	
"E"		[21.6]	[40.1]	[17.5]	[17.5	[26.1]	[38.1]	
		.204	.015	.112	.514	.024	1.323	2.192
Totals	1.836	11.777	2.841	9.160	1.242	10.263	9.753	χ^2 = 46.872

Critical value of χ^2 at 0.05 significance level = 36.4 df = 24

Proceeding one step further, I subtracted the observations of area "A" from the original data and fitted new annual means for the reduced totals. Using only the four subsamples "B" through "E", the appropriate figures from Table 1 for the observed values, and the recalculated annual means for expected values, I assembled a second contingency table (Table 4). Testing the same hypothesis of no sorting in Izembek Lagoon the value of χ^2 (18.043) is in this case not significant at the 0.05 significance level. Area "A" is at Grant Point, the most accessible of all the areas to an observer since it lies at the end of the all-weather road. At present I can offer no explanation for this sorting behavior.

I concluded that sorting did occur in area "A" but not substantially in the other four. In later sections of this manuscript that deal with a hypothetical population and a simulation model I do not include the counts from area "A".

VALIDITY ACCORDING TO FLOCK SIZE

The basic data in Appendix I record a wide range in flock size. To a certain extent this is a consequence of the aggressive posture assumed by family groups (Jones and Jones 1966). The joint defense of family territory, a behavior pattern quite marked in September, results in numerous small flocks consisting of loosely allied

Table 4. Calculation of the Value of χ^2 Using Four Subsamples (Area "A" Deleted) and all Years Beginning with 1964.

Area	1964	1965	1966	1967	1968	1969	1970	Totals
	31.3	17.8	44.7	16.4	16.5	18.7	24.8	
"B"	[25.7]	[19.4]	[41.8]	[16.8]	[17.1]	[21.8]	[34.2]	
	1.220	.131	.201	.009	.021	.440	2.583	4.605
	23.4	18.6	40.8	17.8	15.3	27.6	34.5	
"C"	[25.7]	[19.4]	[41.8]	[16.8]	[17.1]	[21.8]	[34.2]	
	.205	.032	.023	.059	.189	1.543	.002	2.053
	25.1	26.3	42.4	16.6	17.9		44.8	
"D"	[25.7]	[19.4]	[41.8]	[16.8]	[17.1]		[34.2]	
	.014	2.454	.008	.002	.037		3.285	5.800
		19.5	39.3	16.1	20.5	26.9	45.2	
"E"		[19.4]	[41.8]	[16.8]	[17.1]	[21.8]	[34.2]	
		.000	.149	.029	.676	1.193	3.538	5.585
Totals	1.439	2.617	.381	.099	.923	3.176	9.408	$\chi^2 \doteq 18.043$

Critical value of χ^2 at 0.05 significance level = 28.9 $df = 18$

family groups. On the other hand, in Izembek Lagoon there are numerous large flocks of brant characterized by an absence of the strife associated with territorial defense. This raised the question of possible sorting of age classes, and a consequent sorting of the juvenile segment in the population according to flock size.

Addressing this question, I divided the annual samples into three flock sizes: small = 200 birds or less, medium = greater than 200 but less than 500, and large = 500 or more. The results are tabulated in Appendix III, and summarized in Table 5 to show the distribution of flock sizes in the entire set of 161,085 observations.

To test the hypothesis of no sorting according to flock size the data were assembled into a contingency table (Table 6) on the basis of the above divisions. The expected value (in brackets) is the mean percent juveniles in the total sample for the appropriate year, while the observed value is the percent juveniles in the subsample according to flock size. The value of χ^2 is not significant at the 0.05 significance level, and I concluded that the wide range in flock sizes recorded in the annual samples does not discredit their validity as representative of the total population.

CHRONOLOGY

Though the data have been collected during the entire

Table 5. Summary of Brant Observations According to Flock Size.

	Flock size		
	≤ 200	201 - 499	≥ 500
Number of flocks	526	191	72
Percentage of flocks	67	24	9
Total observations	44,293	58,627	58,165
Total juveniles	12,498	15,466	15,233
Percent contribution to total sample	27.5	36.4	36.1
Percent young	28.2	26.4	26.1

Total sample = 161,085
Total juveniles = 43,197
Percent juveniles = 26.8

Table 6. Calculation of χ^2 to Test the Hypothesis of no Sorting of Brant on Izembek Lagoon According to Flock Size.

Flock size:	≤ 200	201 - 499	≥ 500	Totals
1963	22.9 [23.8] .034	21.7 [23.8] .185	26.5 [23.8] .306	.525
1964	24.7 [25.9] .055	25.2 [25.9] .018	29.1 [25.9] .395	.468
1965	28.1 [21.6] 1.956	20.0 [21.6] .118	19.8 [21.6] .150	2.224
1966	48.5 [40.1] 1.760	42.3 [40.1] .121	30.1 [40.1] 2.494	4.375
1967	17.9 [17.5] .009	19.3 [17.5] .185	13.2 [17.5] 1.056	1.250
1968	20.4 [17.5] .481	17.4 [17.5] .001	10.7 [17.5] 2.642	3.124
1969	34.7 [26.1] 2.834	31.5 [26.1] 1.117	23.0 [26.1] .368	4.319
1970	43.0 [38.1] .630	35.7 [38.1] .151	37.9 [38.1] .001	.782
Totals	7.759	1.896	7.412	χ^2=17.067
Critical value of χ^2 at 0.05 significance level = 23.7				*df*=14

period brant were available in each autumn (except for 1963), the total count for the first half of each period is less than that for the second half (Table 7). There are two reasons for the disparity. First, the differing distribution of eelgrass leaves during the two halves of the autumn period, and second, the differing influence of the tide cycle.

The differing distribution of eelgrass leaves derives from the biology of eelgrass, and the windy character of the climate in Izembek Lagoon. In the first half of the autumn period the leaves are rooted to the substrate, but in the second half many leaves are sloughed from the plants and many are torn loose in the rough waters produced by high winds (McRoy 1966). The detached leaves float and gather into large dense mats that drift with wind and tide currents. While the leaves are rooted to the substrate in the first half of the autumn the feeding brant distribute themselves widely over the eelgrass meadows, most of which are not within observing distance from the beaches. However, when the leaves are present in floating mats the birds follow the mats wherever they may drift.

The influence of the tide cycle also changes during the autumn period. In Izembek Lagoon during late spring, summer, and early autumn a low tide exposes the eelgrass beds during daylight hours; but in late autumn, winter,

Table 7. Annual Counts of Brant Recorded on Izembek Lagoon Divided into Two Halves of the Recording Period.

	Early Autumn (~25 Aug to 5 Oct)			Late Autumn (6 Oct to ~8 Nov)		
	Total	% of Annual total	% Juv.	Total	% of Annual total	% Juv.
1964	5,171	26.9	20.7	13,982	73.0	27.9
1965	10,024	30.7	20.5	18,488	69.3	22.3
1966	6,945	34.7	42.9	13,032	65.3	38.6
1967	8,082	41.7	21.4	11,292	58.3	15.4
1968	5,157	24.2	19.9	16,161	75.8	16.8
1969	8,998	42.2	24.3	12,347	57.8	27.6
1970	6,636	25.3	32.9	19,559	74.7	39.9

and early spring such exposures of the eelgrass beds generally occur only during darkness. Tide conditions reach this state in early November, but its effect becomes increasingly evident with the advance of October.

The two factors of (1) floating eelgrass leaves and (2) high diurnal tides combine to render the flocks of feeding brant more available to the observers in the second half of the recording period. The influence of tide currents on movement of the floating eelgrass mats is stronger than that of the wind, carrying the mass towards the beaches (and the observers) on the flooding diurnal tide, and away during the night. The wind adds its influence when the drifting mats approach the beach. If it is an onshore wind a windrow of eelgrass leaves is driven ashore to further attract the birds during the few hours the leaves remain green. Observers took these factors into account and compiled larger numbers in the second half of the recording period than was possible in the first.

Once again χ^2 is appropriate to test for possible sorting in the proportions of juveniles in the subsamples drawn in the two halves of the recording period. The test (Table 8) showed no significance at the 0.05 significance level, and I concluded that the disproportionate subsample from the second half of the autumn does not discredit the use of the total annual sample as representative of the population.

Table 8. Calculation of χ^2 to Compare Proportion of Juveniles in Early Versus Late Autumn.

	Early Autumn ← October 5	Late Autumn October 6 →	Totals
1964	20.7 [25.9] 1.044	27.9 [25.9] .154	1.198
1965	20.5 [21.6] .056	22.3 [21.6] .022	.078
1966	42.9 [40.1] .195	38.6 [40.1] .056	.251
1967	21.4 [17.5] .869	15.4 [17.5] .252	1.121
1968	19.9 [17.5] .329	16.8 [17.5] .028	.357
1969	24.3 [26.1] .124	27.6 [26.1] .086	.210
1970	32.9 [38.1] .709	39.9 [38.1] .085	.794
Totals	3.326	.683	χ^2 = 4.009
Critical value of χ^2 at 0.05 significance level = 12.6			*df* = 6

MARKED BIRDS

In 1965 the staff of the Izembek Range conducted an experiment with marked birds in an attempt to estimate the size of the brant population through application of a "change-in-ratio" estimator. The estimator known in fisheries literature as the "Peterson Method" and in wildlife literature as the "Lincoln Index" (Paulik and Robson 1969) is based on a simple ratio in a marked population:

$$\frac{N}{M} = \frac{n}{m}$$

where N = the unknown population,

M = the number marked,

n = the total number observed,

and m = the total number of marked birds observed. This is a special case of the "mark-recapture" method where marked birds were to be recorded as they were observed on the Wildlife Range while the basic counts proceeded.

Brant were marked in the summer of 1965 at two nesting localities with half inch wide poly-vinyl plastic collars. The plastic was placed around the bird's neck and tied with a jesse knot leaving two streamers about five inches long. On the Yukon River delta, within the Clarence Rhode National Wildlife Range, 1,533 adults and subadults, and 240 juveniles were marked with light-green colored collars (C. J. Lensink personal communication). On the Anderson

River delta, N. W. T. in Canada, 282 adults and 100 juveniles were marked with red collars (T. W. Barry personal communication).

The underlying assumptions in such a model require that:

(1) all birds retain their collars,

(2) all birds, whether marked or unmarked have the same chance of being observed,

(3) all marked birds will be recognized as such, and

(4) the population is closed.

As the counts proceeded and marked birds were recorded when observed, it became apparent that the third assumption was not being fulfilled. The red markers seemed obvious enough, but the green was less evident than expected. The turn around the birds's neck was rarely visible owing to concealment by feathers, and the streamers were often on the side opposite the observer. Unless the bird turned while the observer watched, such a marker was not recorded. On several occasions I performed replicate counts and observed marked birds not observed in the first count.

Moreover, of the 240 green-marked juveniles only one was recorded in the counts. This raised the question of possible collar loss, at least in this segment. The fact of collar loss among the juveniles was confirmed by C. J. Lensink (personal communication), Refuge Manager of the Clarence Rhode Range. Lensink reported some juvenile birds were observed to remove the collar immediately after its application.

At the conclusion of the project 85 marked birds had been observed and recorded in a total count of 32,753 birds.* The marked birds comprised 69 green-collared adults, 10 red-collared adults, 1 green-collared juvenile, and 5 red-collared juveniles. I chose to reject the green-collared juveniles because of collar loss. This left three approaches to solving for N in the ratio. The first was to add the 1,533 green-collared adults to the 382 red-collared birds from Anderson River which yielded an estimate of 746,690. The second was to use only the red-collared birds for an estimate of 834,110. Finally, the third approach was to use the red- and green-collared adults for an estimate of 752,490. These estimates were patently excessive when compared with the previous estimate (see page 16 of this manuscript) of 179,000. Evidently the underlying assumptions were grossly unfulfilled.

A RECAPITULATION

To recapitulate, Section 1 has been a search for

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* The figure 32,753 does not agree with the total recorded from Izembek Lagoon in Appendix II. In that year (1965) counts were also conducted in the Lagoons of Morzhovoi Bay, within the Izembek Range, and are included in the discusiion of marked birds only. The Morzhovoi Bay counts have been possible only at irregular intervals, hence cannot be compared with those from the five areas in Izembek Lagoon.

evidence that the appraisals do not represent the true proportions of juveniles to older birds in the population. Evidence of sorting in the two age classes recorded has been the criterion of the search. The raw data were reduced to first examine the possibility of sorting from place to place within the Lagoon. This revealed that sorting does consistently occur in one area studied, for which no explanation can be offered. Deletion of the counts from this area corrected the difficulty. Second, the data were arranged by flock size and examined for sorting in this parameter. Finally, the data were divided into the first and second halves of the appraisal period and examined for chronological differences. The search furnished no evidence that the appraisals misrepresented the population, which clears the way for use of the appraisals as a management tool.

The process of conducting the appraisals offered, seemingly, the opportunity to add another parameter in assessing the brant population in Izembek Lagoon, and an experiment with a change-in-ratio estimator was conducted. The underlying assumptions could not be met, and this effort proved unsuccessful.

Section 2.

THE OPTIMUM PERIOD FOR DATA GATHERING

THE OPTIMUM PERIOD FOR DATA GATHERING

As a waterfowl inventory technique passes from the research stage into a management practice on a National Wildlife Refuge the matter of manpower-needs demands attention. I have been particularly aware of this as Manager of the Izembek Range where several activities vie for manpower concurrently. This study demonstrates the validity of counts taken at any time in the autumn, conferring the freedom to choose the optimum period for efficient employment of manpower.

The search for such an optimum period has already been narrowed to October so far as the counts were larger than in September (Table 7), and variability was reduced (Table 8). A disadvantage to this period was found in the fact that most brant family groups disintegrated by the end of the first week in October (Jones and Jones 1966). From then until the birds migrate to Mexico there are few opportunities to count family groups (Figure 2), which as the reader may recall, form the basis of an estimate of average family size. These data must be gathered in September.

Wind and visibility constituted the primary limiting factors in securing counts when the birds were within effective range. Average winds for the period 1964 - 1970

Fig. 2. A family group of black brant in Izembek Lagoon.

indicated a slight advantage in the first half of October (Appendix IV), but precipitation in the form of snow squalls occurring in the second half conferred a marked advantage to the first half. Precipitation of any sort reduced visibility, but snow squalls plastered the telescope lenses with snow. Another factor affecting visibility was the amount of solar radiation; not only in intensity, but duration in terms of the length of daylight hours. This declined all fall, but in the second half of October reached limiting values.

In 1970 the idea of gathering data in a short-term, concentrated effort was put to the test. The 10-day period 6th October through 15th was chosen. In that period counts were conducted on six days by two observers for a total of 12,364 observations. This represented 47.1% of the total of 26,195 for that year. The juveniles in the counts for the 10-day period represented 35.6%, a deviation of -2.5 from the 38.1% in the total sample with its standard deviation (of the five area subsamples) of 9.638. Thus the test proved successful.

Section 3.

A HYPOTHETICAL POPULATION

A HYPOTHETICAL POPULATION

The annual appraisals herein reported furnish data from which a hypothetical population of brant may be developed. Such models usually take the form of a record of surviving members of successive cohorts listed in column with the youngest at the top, each separated from the next by an age interval (Hickey 1952). Normally the age interval represents one year.

In most cases dealing with waterfowl the data originate in band returns involving considerable time lag. The Izembek appraisals, however, furnish current data, with more timely interest. Each appraisal provides data which permit immediate division of the sample into three classes: (1) juveniles, (2) reproducing adults, and (3) non-reproducing adults in adult plumage. The first, or youngest, class comes directly from the counts. The remaining birds in the sample, all in adult plumage, represent the adults that reproduced successfully, the adults that did not, and the birds too young to reproduce. (Note, for the purposes of this manuscript "successful reproduction" means production of fully fledged young capable of sustained flight). This remainder may be divided into the second and third classes through the use of the mean family size in the sample. This statistic originates in a record of the number of juveniles in each family group identified as such during the appraisals. This identification was based on numerous papers, beginning with Elder and Elder (1949), which describe distinctive and recognizable goose behavior resulting from family ties. Though most brant do not remain in family groups beyond early October (Jones and Jones 1966), enough family groups may be recorded in Septmeber to furnish a usable mean family size. In the Izembek appraisals this information was first recorded in 1966, and continued to the present. At the conclusion of the 1966 counts a record of 195 families yielded an average family size of 2.86 juveniles per family. Using this number as divisor and the number of juveniles from the four areas "B" through "E" as dividend (7,055) (Appendix V), the quotient (2,466) furnished an estimate of the number of families represented in the sample, and therefore the number of parents (4,932). This was the second class, comprising part of the observed number of birds in adult plumage (9,821), while the balance formed the third class (4,889).

Authorities agree that reproductive success in Arctic nesting geese depends on climatic conditions at the onset and during the time of nesting (Barry 1962, Uspenski 1965). More specifically, snow-free nesting sites adequate for the number of paired adult birds is considered the principal factor. Extensive snow cover leads to poor reproductive success; and the third class listed above, *i.e.*, the non-reproducing birds in adult plumage, includes a large number of adults biologically capable of reproducing in favorable conditions. To date no means of estimating the size of this component has been developed, but in the really reproductively successful seasons its size is minimized. In such years the numbers of reproductively frustrated adults approaches zero sufficiently closely to make the assumption of zero reasonable for the purposes of generating a model population. Acceptance of this assumption means that all adult birds fall in the second class, and all subadults in the third. A second assumption, that no two-year old birds reproduce defines the third class as comprising the yearlings and two-year olds. The case for this assumption is not well established in Arctic nesting geese, especially as there is evidence that two-year old geese do attempt to nest (Barry 1967, Harris and Shepherd 1965, MacInnes 1968), but success in terms of fledged young has not been demonstrated. Sherwood (1967) found that two-year old female giant Canada geese *Branta canadensis maxima* Delacour in their first nesting attempt have their goslings usurped by more experienced adults. Studies with known age Canada geese show that productivity, in terms of fledged young, increases with age to an upper limit (Hanson 1965, Kossack 1950). Collias and Jahn (1959: 503) noted improved productivity in older birds and attributed this to increased dominance acquired with experience.

Reproductive success of brant in 1966 was the highest for which data are available, hence the most suitable to develop a hypothetical population. Converting the three classes of the 1966 sample to a 1,000 bird population, the distribution becomes 418 juveniles, 292 reproducing adults, and 290 non-reproducing birds in adult plumage.

A third necessary assumption is that all birds of breeding age are evenly divided into pairs. Underlying this assumption is another, that equal numbers of both sexes exist in the population. Imber (1968) found that recruitment at hatching in Canada geese comprised equal proportions of sexes, but that males were 1.08 to 1.15 times more vulnerable to hunting mortality than the females. He concluded this vulnerability resulted from the male's larger size, a tendency of the male to initiate flight of a family group, and to lead the flight. This placed the male in a position to be the first target when the flight came within range of gunners, while the following birds swerved and adopted other evasive tactics. Barry (1967) refers to male brant taking the lead in family groups when the brood comes off the nest. My own observations confirm that the larger bird leads when the family group is on the water. In most cases, however, all brant in small flocks take to the air at once and fly in a close pattern such that a gunner's shot charge often finds multiple targets. Moreover, brant do not remain long in family groups (Jones and Jones 1966). Thus the reasons for differential hunting mortality occurring in Canada geese do not seem applicable to brant.

Hunting mortality in brant falls most heavily on the adults (Denson and Murrell 1962), and nearer to the onset of breeding activities than in other North American geese. Denson and Murrell (1962) report the heaviest kill of brant in Humboldt Bay in the last 2½ weeks of a hunting season that closed the 20th of February 1958. Similar reports were furnished in personal communications concerning brant hunting in British Columbia by Robert D. Harris and William Morris, both of the Canadian Wildlife Service in Vancouver. In British Columbia the hunting season closed in 1972 on March 10. The point of this discussion is that it relates to the third assumption above, that all birds of breeding age are evenly divided into pairs, and the question of re-mating of individuals from broken pairs before the onset of nesting. No data are available for brant, but observers (Jones and Obbard 1970, Sherwood 1967) have reported accelerated pairing in adult Canada geese that had lost their mates; and Harrison (1967) reports a case of a bigamous graylag gander *Anser anser* L. that abandoned his nesting mate, immediately remated and assisted in rearing the new brood. The close association maintained by brant on the northward migration seems likely to furnish the opportunity for surviving members of broken pairs to find new mates before reaching the nesting grounds.

Several hypothetical age distributions exist for various populations of Canada geese (Hanson 1965, Grieb 1970, Chapman *et al* 1969). One of these, Grieb's model for the February 1966 shortgrass prairie Canada goose population showing a hypothetical 40% young, closely approximates the brant sample of fall 1966. Separated into age classes similar to those in the brant sample, a one thousand bird population of these Canada geese consists of 400 juveniles, 304 non-breeding birds in adult plumage, and 296 breeding adults, *vis a vis* 418, 290, 292 for the brant. With such close initial agreement I used Grieb's age distribution as a starting point, but compressed his 14 year classes into 7 by lumping the 8 eldest into 1. Thus the year classes as used herein appear as 0-1, 1-2, 2-3, 3-4, 4-5, 5-6, and 6 or older. As already defined the final four are the reproductive classes. With this age distribution, and observing the rule that reproductive success improves with experience, which is to say, age, I searched for reproduction rates that agreed with the observed facts, *i.e.*, reproduction capable of yielding exactly 418 young in a population of 292 adults forming 146 pairs on the nesting ground. With these pairs distributed in year classes such that there were 44 in the fourth class, 31 in the fifth class, 22 in the sixth, and 49 in the seventh, the required production rates per pair were 1.8, 2.5, 3.0, and 4.0 respectively. I reached these conclusions by noting the constraints of (1) a given number of producers [146 pairs], (2) a given total production [418], and (3) a given mean production rate [the mean number of juveniles in families: 2.86]. The age distribution and production rates listed above meet these three constraints. They represent averages, of course, since the family group counts appear as integers ranging from one through six.

Henny *et al* (1970) point out that questions concerning wild animal populations may be examined through a simulation model using the parameters of mortality rates, age at which the species begins to reproduce, the recruitment rate schedule, and the age ratios in the population. Three of these parameters have been adduced in the case of the brant population for a given set of conditions, *i.e.*, the population at Izembek Lagoon in fall 1966.

The objective in such a simulation model is to determine the size of a population and its age distribution at some future date or dates while varying the factors influencing total numbers. Beginning in Izembek Lagoon in fall on the eve of migration to the wintering grounds, the brant population has completed its cycle of reproduction and will experience no increase until it returns north in spring. In that interval natural mortality functions to reduce the population on the long migration both ways, plus the period of rest between. To natural mortality is added hunting mortality. When once again the population reaches the nesting ground a period of increase is at hand, while mortality continues. It takes many forms affecting every class from maturing ova through moulting adults, and in the southbound flight to Izembek Lagoon hunting mortality is again added. This mortality may be entered in a simulation model at every stage in the annual cycle as it occurs, if it can be measured or estimated, but since its effect is cumulative it can be entered at one point - greatly simplifying the model. Recruitment, as measured in the Izembek appraisals, is net production. Choosing this point in time to measure recruitment avoids the difficulties of estimating the various factors governing successful reproduction, but simply measures the end product when it is complete. This furnishes a convenient anniversary date for the model, a discrete date at which the model describes the population.

The Leslie model (Leslie 1945, 1948) provides a mathematical system for handling these parameters of recruitment and survival given a population of known age distribution. The formulae used in this manuscript with seven year classes are:

$$p'_0 = \Sigma\, p_0 r_0 + p_1 r_1 \ldots p_6 r_6$$
$$p'_1 = p_0 s_0$$
$$\cdot$$
$$\cdot$$
$$p'_6 = p_5 s_5 + p_6 s_6$$

where p_i is the number of brant of age i at time t, p'_i is the number of brant of age i at anniversary date $t + 1$ year, $r_0 \ldots r_6$ are age specific recruitment rates, and $s_0 \ldots s_6$ age specific survival rates.

In the model (Appendix VI) each year class moves into the next class as the anniversary date is reached, leaving the first class (p'_0) to be filled by recruitment. The sixth class (p_5) moves into the seventh (p'_6), hence is added to the surviving segment of the earlier seventh (p_6) class. As herein used, mortality includes both natural and hunting mortality, and appears in the model as a survival rate where s= 1.00 minus mortality. It should be noted here that lumping all year classes beyond the sixth into one class stems from an inability to distinguish these older classes with the available data. I have assumed that mortality beyond p_6 is sufficiently constant to permit such lumping.

The simulation process is illustrated in Table 9 using the hypothetical 1,000 bird population for 1966 as the starting population, mortality of 30% across all year classes, and the recruitment rates developed for 1966. The recruitment rates are expressed as the number of young produced per bird, made necessary by defining the population in terms of individual birds rather than pairs.

Numerous uses for the model might be suggested, but for the present purposes I offer three. (1) Are current band return data a reliable guide to mortality? (2) Given a management policy, say, to continue hunting while permitting a slow rise in brant numbers, what is the allowable mortality? (3) How should recruitment data expressed as a ratio be viewed?

To address the first question I assembled available banding data. Banding of brant on the Yukon - Kuskokwim Delta began in 1949 and has continued with but two breaks, one of 6 years and another of 1, until the present. The number of banded birds at the end of operations in 1970 reached 23,982. Of these 2,088 have been recovered by brant hunters. These recoveries were fitted into life tables limited to the 4 years subsequent to banding. This seemed advisable because of excessive band loss experienced until the metal in the band was changed from an aluminum alloy to monel (C. J. Lensink, personal communication). The choice of 4 years was arbitrary, since the rate of loss is not

Table 9. One Year Simulation of the Black Brant Population Using the Leslie Matrix Model, and an Age Structure Based on the Fall 1966 Population in Izembek Lagoon.

Year class	Age structure		Survival		Spring pop. on nesting grounds		Recruitment rates/bird		Production	New fall population
0-1	418	x	0.7	=	292.6	x	0	=	0	→ 293
1-2	165	x	0.7	=	115.5	x	0	=	0	293
2-3	125	x	0.7	=	87.0	x	0	=	0	116
3-4	88	x	0.7	=	61.6	x	0.9	=	55.4	87
4-5	62	x	0.7	=	43.4	x	1.25	=	54.2	62
5-6	44	x	0.7	=	30.8	x	1.5	=	46.2	43
6+	98	x	0.7	=	68.6	x	2.0	=	137.2	99
Totals	1,000								293.0 →	993

known. No composite tables were constructed. The mean mortality calculated from nine cohorts of adults was 46.5% (Appendix VII). Because of relatively few bandings of juvenile or yearling birds few recovery data are available.

Data used in the model were the hypothetical population figures for 1966 including the age structure (P_t) and recruitment rates. The survival rates were based on the mean mortality of 46.5% calculated from band returns. A simulation representing four years resulted in a decline from 1,000 birds to 325 (see Appendix VIII for simulation runs). No such rapid decline has been observed in the real population of brant, hence the unweighted application of band recovery data seems unwarranted.

I then considered question two and searched for the "break even" point of mortality, while still using the 1966 data including recruitment rates. The reader should bear in mind that the 1966 recruitment rates are the highest yet recorded, which explains why I have not used higher rates in these simulations. The "break even" point was found to lie between 68% and 69% survival. At 68% the population declined slowly, but none-the-less steadily. At 69% an initial 3 year decline reversed itself so that the population slowly rose. The survival rate thus determined represents the most optimistic circumstances because of the high recruitment rates employed. To approach a more realistic set of conditions I varied recruitment rates in a cyclic order of three years, using for the first year the 1966 conditions, for the second (to simulate poor recruitment) rates per adult pair of 0.2, 1.8, 2.5, 3.0, and in the third (intermediate recruitment) 0.6, 2.4, 2.4, 3.0. In this simulation the population gradually declined at a survival rate of 70%, and increased when survival was raised to 75%. These simulations are recorded in Appendix VIII.

The model does not distinguish natural mortality from the hunting form, but it does define the limit where an increasing population changes to a declining one. Moreover, when available estimates of population size and of recruitment are employed in the model it can reveal how closely the regulating factors lie to the critical changeover point.

Regarding the third question, Lynch and Singleton (1964) and Grieb (1970) point out the need for careful analysis of appraisal data expressed as a ratio, such as percentages. For example, a year of high reproductive success results in a large yearling class the following year, and since these birds cannot reproduce, the recruitment for the second year expressed as a percentage of the population must necessarily be less than that for the first. This is true even if the recruitment in the second year is numerically equal to the first. Two successive years with high percentages of young in the population would indicate the intervention of high mortality in some year classes, probably the second or third, or both. The model quickly demonstrated that steady or slightly rising percentages of young in a brant population was symptomatic of a declining population.

Section 4.

CONCLUSION

CONCLUSION

The question uppermost in my mind relates to the effect of the spring hunting on the age distribution in the black brant population. In 1972 hunting ceased in Humboldt Bay, California February 22, and in British Columbia March 10. Denson and Murrell (1962) suggest that adults precede the non-breeding birds on the north bound migration, beginning in late January, and therefore sustain the heaviest hunting mortality. They report the conclusion, on the basis of bag checks in 1957-58, 1958-59, and 1959-60, that adult brant greatly outnumbered immature birds.

The model can furnish answers to the question of age distribution. Without "real life" data it can only define limits, but as more and more of the "real" numbers become available the limits of the remaining variables become narrower.

The usual grand design for a waterfowl population such as the black brant is the attainment of maximum sustainable yield without introducing conflict with other values. In waterfowl management conflict generally arises in the form of depredation on agricultural crops or in competition with other species. In a marine species, such as the brant, these conflicts appear unlikely. There have been rare examples, such as grazing on pasture adjacent to Humboldt Bay, and in the years when eelgrass was commercially harvested on the Atlantic coast its use by brant was considered an infringement by some (Lewis 1931). Generally, however, the goal of maximum sustainable yield in brant can be considered without the element of conflict.

The two curves of recruitment and mortality then become the parameters defining the limits within which maximum sustainable yield may be achieved. Natural mortality has never been estimated in brant, and this study deals with total mortality without suggesting a means to distinguish between natural and hunting mortality. The thrust of this study is to estimate recruitment. In a population that has been hunted for many years; and which, given the present circumstances, will likely experience continued hunting; the ideal of starting with the two basic curves to determine maximum sustainable yield is not possible. In such a case the two knowable parameters are recruitment and hunting mortality, and in Arctic nesting geese only the latter can be managed.

In brant the upper limit to population size is unknown, but historical records indicate a potential of at least twice the present population (Smith and Jensen 1970). Therefore, long-range management of the black brant seems to require a policy of balancing hunting mortality with annual recruitment to allow an upward trend in the size of the population. This is not accomplished in the present practise of basing management on a January inventory that is over a year old before the major harvest requiring regulation falls on the population. This peculiar situation develops from the fact that the heaviest hunting mortality in the U. S. and Canada occurs in February and March, but the regulations are promulgated in the preceding fall. This late hunting season occurs because the bulk of the brant population proceeds directly to Mexico from Izembek Lagoon and does not appear in the U. S. and Canada until late February and March. The reproductive potential of black brant is sufficient to restore the population to its upper limits without unduly restrictive regulation. It does, however, require a policy that hunting harvest be such that total mortality is held below annual recruitment for several years. Herein lies the strength of this study, for it demonstrates one system of accurately estimating recruitment for the entire population.

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Appendix I. Basic flock data.

Date	Area	Flock total	No. juveniles
Oct 23 1963	C	94	16
	C	125	20
	C	136	15
	C	124	9
	C	205	26
	C	38	12
	C	79	15
	C	140	58
	C	151	16
Oct 24 1963	C	213	34
	C	346	40
	C	52	11
	C	313	82
	C	31	8
	C	251	55
Oct 25 1963	D	304	117
	D	48	13
	D	150	61
	D	513	117
	D	58	17
	D	111	35
	D	47	13
	D	84	25

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Oct 28 1963	D	818	239
	D	193	36
	D	587	153
Sept 17 1964	D	189	16
	D	347	67
	D	499	82
	D	140	36
	D	144	25
	D	209	29
	D	389	30
	D	51	8
	D	236	23
	D	22	4
Sept 25 1964	B	67	18
	B	12	2
	B	17	9
	B	306	106
	B	206	60
	B	231	51
	B	206	81
Sept 29 1964	C	123	31
	C	190	47
	C	12	3

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Sept 29 1964	C	398	63
	C	186	54
	C	29	11
	C	122	14
	C	150	27
	C	102	22
	C	493	143
	C	19	3
	C	13	5
	C	63	3
Oct 9 1964	A	156	70
Oct 11 1964	A	19	8
	A	59	18
	A	58	9
	A	50	6
	A	38	3
	A	5	3
	A	34	14
	A	33	3
	A	28	1
	A	63	5
	A	108	54
	A	20	13

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Oct 12 1964	A	27	13
	A	6	4
	A	59	17
	A	20	8
	A	125	26
	A	21	5
	A	43	12
	A	21	6
	A	4	2
	A	23	11
	A	42	17
	A	79	26
	A	87	25
	A	69	12
Oct 13 1964	A	122	26
Oct 22 1964	B	968	372
	B	1164	267
	C	324	81
	C	125	45
	C	59	16
	C	259	59
	C	187	35
	C	44	12

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Oct 22 1964	C	75	18
	C	53	9
	C	161	44
	C	74	25
Oct 23 1964	B	293	113
	B	147	52
	C	120	17
	C	38	6
	C	57	12
	C	130	32
	C	176	66
	C	102	35
	C	368	99
	C	47	9
	C	742	125
	C	334	53
Oct 27 1964	D	65	39
	D	736	273
	D	443	170
	D	1032	315
	D	295	94
	D	476	173
	D	290	107

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Oct 27 1964	C	354	142
	C	141	61
	C	20	10
	C	123	17
	C	101	21
	C	158	65
	C	56	32
Nov 2 1964	D	197	33
	D	211	31
	D	158	24
	D	340	28
Nov 5 1964	C	169	13
	C	77	13
	C	122	7
	C	153	16
	C	30	10
	D	61	11
	D	206	61
	D	54	18
	D	39	8
	D	61	18
	D	90	29
Nov 9 1964	C	192	28

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Nov 9 1964	C	57	12
	B	9	5
Sept 3 1965	D	220	30
Sept 13 1965	B	925	166
	C	177	16
	C	86	25
	C	49	21
	C	5	2
Sept 14 1965	A	5	3
	A	6	4
	A	4	2
	A	56	27
Sept 15 1965	C	69	0
	C	62	2
	C	22	2
	C	49	2
	B	407	12
	B	261	21
	B	330	12
	B	175	8
Sept 20 1965	A	54	22
	A	90	37
	A	191	66

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Sept 20 1965	A	13	8
	A	136	44
Sept 23 1965	A	489	180
	A	73	44
	A	15	8
Sept 24 1965	D	47	11
	D	115	42
	D	3	1
	D	126	39
	D	120	42
	D	136	36
	D	4	2
	D	7	5
	D	5	3
	D	40	3
	D	628	126
Sept 27 1965	A	14	1
	A	4	2
	A	4	2
	A	3	2
	A	209	37
	A	113	19
	A	39	10

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Sept 28 1965	A	34	18
	A	69	21
	A	27	8
	A	538	194
Sept 29 1965	A	59	19
	C	75	24
	C	88	7
	C	12	7
	C	22	0
	C	4	2
Sept 30 1965	A	78	34
	E	271	59
	E	12	4
	E	67	8
	E	210	53
	E	244	59
Oct 4 1965	B	1279	187
	B	458	112
	B	487	33
	B	27	12
	B	78	17
	B	270	34
	B	29	5

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Oct 6 1965	A	39	16
	A	199	87
Oct 8 1965	B	237	79
	B	40	5
	B	262	48
	B	132	16
	C	44	13
	C	285	65
	E	861	179
Oct 9 1965	E	39	9
	E	62	18
	E	44	18
	E	31	5
	E	190	32
	E	39	11
	E	34	6
	E	23	7
	E	48	15
	E	16	4
	E	20	9
	E	96	22
	E	51	22
	E	773	73

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Oct 10 1965	B	6	4
Oct 13 1965	B	149	6
	C	236	31
	C	181	23
	C	19	13
	C	133	23
	C	236	45
	C	349	67
	C	672	101
	C	113	27
Oct 14 1965	A	215	103
	A	96	25
	A	8	4
Oct 15 1965	D	101	56
	D	87	33
	D	33	1
	D	616	123
	A	229	59
	C	37	10
	A	75	31
Oct 18 1965	C	520	123
	C	427	52
	C	244	28

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Oct 18 1965	C	148	29
	C	279	54
	C	199	41
	C	268	36
	C	322	42
	C	172	40
	C	453	84
	B	18	8
	B	24	9
	B	461	179
	B	199	75
	A	21	11
	A	4	1
	A	1	0
	A	18	5
	A	108	49
	A	20	8
	A	29	12
Oct 19 1965	C	103	19
	C	262	71
	C	681	153
	C	65	11
	C	122	29

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Oct 20 1965	C	508	109
	C	547	140
	C	595	163
	A	74	21
	B	95	39
	B	758	203
	B	651	119
	B	343	39
Oct 21 1965	D	402	92
	D	121	91
	D	162	48
	C	718	134
	C	801	64
Oct 22 1965	A	300	99
	A	89	40
Aug 31 1966	A	703	16
	A	43	5
Sept 3 1966	A	152	31
	A	27	8
Sept 7 1966	A	498	179
Sept 11 1966	A	151	61
	A	34	18
Sept 16 1966	A	438	137

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Sept 16 1966	A	47	24
	A	116	71
	A	337	115
	B	166	62
	B	70	31
Sept 19 1966	A	38	8
	A	60	24
	A	35	19
	A	19	12
	D	270	45
	D	152	75
Sept 22 1966	B	45	26
	B	1088	299
	B	191	110
Sept 26 1966	A	403	228
	C	107	59
	C	63	33
	C	222	105
	C	14	6
	C	34	21
Sept 29 1966	B	640	281
	B	831	384
	B	326	87

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Sept 29 1966	B	231	88
	B	64	36
Oct 4 1966	C	176	50
	C	146	49
	C	136	46
	C	89	32
Oct 7 1966	D	136	70
	D	140	71
	D	280	136
	D	70	29
	D	637	187
	D	97	39
	C	1045	263
	C	218	61
	C	156	50
Oct 14 1966	E	373	133
	E	339	140
	E	102	42
	E	386	176
	E	245	90
	E	161	80
	E	289	127
	E	354	78

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Oct 14 1966	E	205	78
Oct 16 1966	E	67	24
	E	43	14
	E	319	104
	E	518	181
	E	785	268
	E	364	136
	E	248	92
	E	98	54
	E	90	35
	E	473	213
	E	349	136
Oct 19 1966	B	321	185
	B	143	94
	B	119	64
	B	146	87
	B	333	175
	C	100	63
	C	64	42
	C	128	74
	C	163	95
	C	62	39
	C	119	71
	C	109	69

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Oct 19 1966	C	39	23
Oct 21 1966	C	128	64
	C	49	31
	C	105	51
	C	29	20
	C	90	50
	D	88	44
	D	275	111
Oct 24 1966	B	167	105
	B	461	279
Aug 23 1967	A	12	6
Aug 28 1967	D	152	43
	D	129	27
	D	27	5
	D	6	4
	D	57	5
Sept 11 1967	A	37	14
	A	55	30
	A	30	10
Sept 12 1967	A	132	34
	A	133	53
	A	61	9
	A	34	14

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Sept 12 1967	D	41	17
	D	23	8
	D	74	21
	D	10	2
Sept 19 1967	C	335	75
	C	298	77
	C	91	29
	C	29	16
	C	221	67
	C	139	45
	C	299	96
	A	178	60
Sept 22 1967	B	299	79
	B	72	16
	C	34	12
	C	76	21
	C	62	15
	C	23	5
	C	102	17
	C	159	25
	C	59	15
	C	28	8
Sept 25 1967	D	263	56
	D	118	15

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Sept 25 1967	D	138	13
	D	293	44
	D	71	2
	D	84	4
	D	22	11
Sept 26 1967	C	155	29
	C	385	73
	C	146	34
	C	280	26
	C	125	18
	C	73	4
	C	67	3
Sept 27 1967	B	182	7
	B	342	13
	B	92	3
Sept 28 1967	B	365	65
	B	66	29
	B	383	82
	B	127	20
	B	85	9
	B	245	121
Oct 3 1967	D	30	18
Oct 5 1967	C	43	4

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Oct 5 1967	C	385	49
Oct 7 1967	B	95	3
Oct 9 1967	B	169	26
	B	208	28
	B	574	123
	B	445	89
	B	526	65
	E	172	10
	E	473	68
	E	57	30
	E	154	45
	E	85	17
	E	60	1
	E	46	9
	E	159	26
	E	53	0
	E	36	9
	E	102	8
	E	213	81
Oct 10 1967	A	56	12
	D	187	13
	D	10	2
	D	123	13
	D	51	1

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Oct 10 1967	D	36	0
Oct 13 1967	E	210	24
	E	84	22
	E	183	21
	E	24	3
	E	212	29
	E	66	4
	E	550	46
Oct 19 1967	B	375	41
	C	39	3
	C	206	28
	C	63	8
	C	70	5
	C	157	17
	C	32	5
	C	100	14
	C	96	14
	C	154	18
	C	77	8
	C	42	0
	C	174	19
	C	77	7
Oct 20 1967	B	516	52

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Oct 20 1967	B	381	54
	B	62	11
	B	106	25
Oct 22 1967	A	103	18
	A	58	17
	A	42	10
Oct 23 1967	A	26	3
	A	66	16
Oct 24 1967	C	65	6
	C	23	3
	C	66	6
Oct 25 1967	E	58	11
	E	59	19
	E	174	25
	E	107	21
	E	104	21
	E	108	24
	E	46	5
	E	212	40
	E	302	65
	E	152	14
	E	212	16
	E	120	27

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Oct 26 1967	A	51	17
Oct 27 1967	C	117	22
	C	328	32
	C	100	24
	C	182	19
	C	86	24
Nov 2 1967	B	179	10
Aug 23 1968	A	60	5
	A	79	8
	A	15	9
	A	10	6
	A	12	5
	A	13	5
	A	7	5
Sept 4 1968	B	3	1
Sept 6 1968	A	425	97
	A	355	49
	A	385	91
	A	57	15
	A	19	8
	A	22	7
Sept 17 1968	C	340	47
	C	327	45

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Sept 17 1968	C	53	10
Sept 26 1968	B	542	62
	B	121	66
	B	86	43
	B	159	81
	B	176	65
Oct 2 1968	C	279	49
	C	313	56
	C	179	23
	C	223	23
	C	359	53
	C	106	12
	C	52	7
	C	78	12
	B	302	61
Oct 7 1968	C	119	6
	C	204	52
	C	105	32
	C	185	26
	C	124	7
	C	129	7
	C	174	11
	C	236	36

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Oct 11 1968	D	17	6
Oct 14 1968	E	104	12
	E	189	24
	E	102	15
	E	55	11
	E	163	22
	E	203	39
	E	68	14
	E	73	15
	E	55	9
	E	142	22
	E	35	10
Oct 15 1968	E	116	26
	E	110	23
	E	317	56
	E	79	2
	E	111	18
	E	321	96
	E	45	13
	E	116	30
	E	92	33
	E	224	75
	E	58	5

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Oct 15 1968	B	56	3
	B	216	60
	B	124	24
Oct 16 1968	D	95	14
	D	36	17
	D	141	44
	D	67	17
	B	27	4
	B	173	9
	B	157	14
	B	56	5
	B	455	14
	B	707	50
	B	31	14
Oct 17 1968	C	37	11
	C	171	49
	C	75	17
	C	70	11
	C	214	54
	C	100	16
	C	183	42
	C	115	25
	C	24	5

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Oct 17 1968	C	29	2
Oct 18 1968	C	40	6
	C	235	36
	C	422	45
	C	296	32
	C	65	4
	C	94	17
Oct 23 1968	A	294	41
	A	357	53
	A	214	12
	A	236	42
	A	123	17
	A	64	16
Oct 25 1968	A	67	21
Oct 27 1968	A	64	19
	A	12	3
Oct 28 1968	A	51	25
	A	36	19
Oct 29 1968	D	523	51
	D	86	26
	D	189	33
Oct 30 1968	D	45	9
	D	99	17

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Oct 30 1968	D	37	3
	D	284	32
	D	137	5
	D	42	10
	D	26	7
Oct 31 1968	B	620	59
	B	96	10
	B	303	64
	D	112	15
	D	205	29
	D	287	32
	D	266	26
Nov 1 1968	B	67	8
	B	609	99
	B	122	33
	B	179	39
	B	131	17
	B	282	56
	D	299	86
	D	335	72
	D	145	43
	D	215	42
	D	206	64

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Nov 3 1968	A	114	46
Sept 3 1969	A	20	10
Sept 4 1969	A	628	112
Sept 11 1969	A	266	117
Sept 22 1969	B	1127	193
Sept 23 1969	A	512	252
Sept 24 1969	B	809	142
Sept 29 1969	A	101	42
Sept 30 1969	B	3278	514
Sept 31 1969	A	746	349
Oct 1 1969	B	373	113
Oct 2 1969	A	182	113
	A	110	57
Oct 3 1969	B	846	170
Oct 6 1969	A	276	110
Oct 7 1969	C	31	10
	C	49	15
	C	32	9
	C	73	38
	C	265	57
Oct 9 1969	C	158	30
	C	119	28
	C	283	64

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Oct 9 1969	C	112	30
	C	159	41
	C	264	73
Oct 13 1969	A	334	138
Oct 14 1969	E	268	100
	E	101	29
	E	262	59
	E	206	38
	E	46	8
	E	329	93
	B	1253	232
	B	366	59
Oct 15 1969	A	348	144
Oct 16 1969	B	237	92
Oct 17 1969	A	525	209
Oct 22 1969	C	1703	503
Oct 27 1969	B	180	47
	B	753	178
	B	1302	212
	B	160	52
	C	259	66
	C	183	48
	C	763	209

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Oct 27 1969	C	57	25
Oct 28 1969	A	82	34
Oct 29 1969	A	68	29
Oct 30 1969	A	109	44
	A	435	181
Oct 31 1969	A	5	0
Nov 20 1969	A	192	69
Aug 21 1970	A	30	6
Sept 16 1970	A	29	12
Sept 17 1970	A	107	30
	A	40	19
	A	467	157
Sept 18 1970	A	81	44
	B	327	113
Sept 19 1970	A	303	131
Sept 20 1970	B	756	56
	B	474	114
	A	1089	467
Sept 21 1970	B	531	151
	B	342	85
	B	395	124
	B	414	114

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Sept 21 1970	A	23	14
Sept 22 1970	A	57	26
Sept 29 1970	A	550	260
Oct 1 1970	A	586	236
Oct 2 1970	A	35	25
Oct 7 1970	B	1005	263
Oct 8 1970	E	54	24
	E	102	47
	E	126	47
	E	346	158
	E	143	66
	E	202	87
	E	133	45
	E	176	98
	E	337	152
	E	120	47
	E	65	30
	E	144	51
	E	235	93
	E	70	35
	E	317	153
	E	208	116
	E	139	74

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Oct 8 1970	E	226	107
	E	103	26
	E	68	43
Oct 9 1970	C	236	66
	C	240	38
	C	533	188
	C	224	59
	C	902	287
	C	157	76
	C	840	307
Oct 10 1970	E	78	42
	E	97	38
	E	124	56
Oct 11 1970	C	1669	503
	C	107	43
	C	190	69
	C	110	41
	C	63	27
	C	49	21
Oct 12 1970	B	402	69
	C	521	201
	C	100	27
	C	188	70

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Oct 12 1970	C	349	131
	C	152	67
	C	348	133
	C	205	67
	C	161	22
Oct 16 1970	A	205	93
Oct 19 1970	A	81	57
	A	64	35
Oct 20 1970	A	200	105
	B	238	87
	B	528	168
Oct 21 1970	A	550	256
Oct 22 1970	D	29	9
	A	101	79
Oct 23 1970	A	2109	1154
	D	338	153
Oct 25 1970	A	63	31
Oct 27 1970	A	5	3
Oct 28 1970	C	518	255
Oct 29 1970	A	76	36
	C	598	232
Oct 31 1970	A	590	270
Nov 2 1970	A	181	73

Appendix I. (continued).

Date	Area	Flock total	No. juveniles
Nov 2 1970	A	13	2
Nov 3 1970	D	178	85
Nov 5 1970	D	65	23
Nov 7 1970	D	306	141
Nov 11 1970	C	159	46

Appendix II. Summary of basic flock data. Numbers of juveniles and total numbers of birds are listed for the five areas for eight years.

Year	Area "A"		Area "B"		Area "C"		Area "D"		Area "E"	
	Juveniles	Total	Juveniles	Total	Juveniles	Total	Juveniles	Total	Juveniles	Total
1963	-	-	-	-	417	2,298	826	2,913	-	-
1964	417	1,419	1,136	3,626	1,671	7,128	1,752	6,980	-	-
1965	1,383	3,848	1,448	8,101	1,950	10,459	784	2,973	613	3,131
1966	956	3,101	2,393	5,342	1,467	3,591	907	2,135	2,288	5,808
1967	323	1,074	971	5,894	1,045	5,868	324	1,945	741	4,593
1968	624	3,091	961	5,800	886	5,755	700	3,894	570	2,778
1969	2,010	4,939	2,004	10,684	1,246	4,510	-	-	327	1,212
1970	3,621	7,635	1,344	5,412	2,976	8,619	411	916	1,635	3,613

Appendix III. Brant observations recorded on Izembek Lagoon distributed according to flock size.

Flock size:	≤ 200			201 - 499			≥ 500		
Year	Juv.	Total	% Juv.	Juv.	Total	% Juv.	Juv.	Total	% Juv.
1963	380	1,661	22.9	354	1,632	21.7	509	1,918	26.5
		17 Flocks			6 Flocks			3 Flocks	
1964	1,678	6,798	24.7	1,946	7,713	25.2	1,352	4,642	29.1
		85 Flocks			24 Flocks			5 Flocks	
1965	1,906	6,775	28.1	1,915	9,666	20.0	2,347	12,071	19.8
		103 Flocks			31 Flocks			17 Flocks	
1966	2,511	5,173	48.5	3,621	8,557	42.3	1,879	6,247	30.1
		54 Flocks			26 Flocks			8 Flocks	
1967	1,600	9,038	17.7	1,518	8,170	18.5	286	2,166	13.2
		106 Flocks			27 Flocks			4 Flocks	
1968	1,608	7,883	20.4	1,812	10,434	17.4	321	3,001	10.7
		91 Flocks			36 Flocks			5 Flocks	
1969	808	2,329	34.7	1,504	4,771	31.5	3,275	14,245	23.0
		23 Flocks			16 Flocks			13 Flocks	
1970	1,992	4,636	43.0	2,741	7,684	35.7	5,254	13,875	37.9
		47 Flocks			25 Flocks			17 Flocks	

Appendix IV. Wind speeds in the month of October at Izembek Lagoon, 1964 - 1970. Data from U. S. Weather Bureau.

Date	Average speed (mph)	Average fastest mile	Date	Average speed (mph)	Average fastest mile
1	16.5	29.7	16	13.0	22.7
2	16.4	28.4	17	11.9	23.3
3	12.6	23.3	18	15.6	28.1
4	20.2	32.9	19	16.9	29.6
5	14.6	27.6	20	10.3	22.0
6	15.6	28.4	21	15.8	28.3
7	17.3	31.4	22	15.9	25.7
8	17.9	29.3	23	13.9	27.1
9	14.9	24.4	24	16.1	28.4
10	12.7	22.4	25	10.5	21.4
11	12.8	24.7	26	18.9	31.1
12	17.0	27.1	27	14.2	27.6
13	15.4	27.9	28	17.9	29.4
14	14.7	26.6	29	17.4	30.3
15	15.9	26.1	30	18.7	33.1
			31	24.0	35.4

Average wind speed		Fastest mile	
Monthly mean, average wind speed		Monthly mean, fastest mile	
15.66 mph	$\sigma = 2.83$	27.53 mph	$\sigma = 3.43$
Mean, average speed 6th - 15th		Mean, fastest mile 6th-15th	
15.42 mph	$\sigma = 1.74$	26.83 mph	$\sigma = 2.60$
Mean, average speed 16th - 31st		Mean, fastest mile 16th-31st	
15.69 mph	$\sigma = 3.47$	27.71 mph	$\sigma = 3.95$

Appendix V. Division of the 1966 Izembek sample into three classes: juveniles, reproducing adults, and non-reproducing birds in adult plumage.

Calculation of mean family size

Number juveniles per family	Number of families	Total number juveniles
1	31	31
2	44	88
3	66	198
4	34	136
5	16	80
6	4	24
	195	557

$$\text{Mean number of juveniles per family} = \frac{557}{195} = 2.86$$

Standard error = .088

$$\text{Number families represented} = \frac{\text{number juveniles}}{\text{mean family size}} = \frac{7,055}{2.86} = 2,466$$

Reproducing adults = number families x 2 = 2,466 x 2 = 4,932

$$\text{Percent juveniles} = \frac{\text{number juveniles}}{\text{sample total}} = \frac{7,055}{16,876} = .418$$

$$\text{Percent reproducing adults} = \frac{\text{number adults}}{\text{sample total}} = \frac{4,932}{16,876} = .292$$

Percent non-reproducing birds in adult plumage = 1.00 - .418 - .292 = .290

Appendix VI. The Leslie model in mathematical notation. (Leslie 1945, 1948).

Year class	0-1	1-2	2-3	3-4	4-5	5-6	6+		P_t		P_{t+1}
0-1	r_0	r_1	r_2	r_3	r_4	r_5	r_6		p_0		p'_0
1-2	s_0								p_1		p'_1
2-3		s_1							p_2		p'_2
3-4			s_2					x	p_3	=	p'_3
4-5				s_3					p_4		p'_4
5-6					s_4				p_5		p'_5
6+						s_5	s_6		p_6		p'_6

$$p'_0 = \Sigma\, p_0 r_0 + p_1 r_1 \ldots p_6 r_6$$

$$p'_1 = p_0 s_0$$

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$$p'_6 = p_5 s_5 + p_6 s_6$$

Where P_t is a column vector of numbers of brant of ages 0, 1, . . . 6+ at time t, P_{t+1} a column vector of brant at anniversary date t + 1 year, $r_0 \ldots r_6$ are age specific recruitment rates, and $s_0 \ldots s_6$ age specific survival rates.

Appendix VII. Four-year life tables for adult black brant based on banding returns.

Years survived	Alive at start	Number shot	Mort. rate	Alive at start	Number shot	Mort. rate
		1950			1951	
0-1	89	34	.382	70	28	.400
1-2	55	26	.473	42	16	.381
2-3	29	13	.448	26	16	.615
3-4	16	16		10	10	
	189	89	.471	112	70	.625
		1952			1954	
0-1	65	18	.277	64	13	.203
1-2	47	19	.404	51	22	.431
2-3	28	7	.250	29	20	.670
3-4	21	21		9	9	
	161	65	.404	153	64	.418
		1961			1962	
0-1	60	7	.117	192	49	.255
1-2	53	18	.340	143	71	.497
2-3	35	18	.514	72	39	.542
3-4	17	17		33	33	
	165	60	.364	440	192	.436
		1963			1965	
0-1	202	89	.441	136	66	.485
1-2	113	43	.381	70	21	.300
2-3	70	33	.471	49	29	.592
3-4	37	37		20	20	
	422	202	.479	275	136	.495
		1967				
0-1	35	13	.371			
1-2	22	9	.409			
2-3	13	12				
3-4	1	1				
	71	35	.493			

Mean = .465

σ = .0745

Appendix VIII. Simulation with the population model. Each run starts with a population of 1,000 birds, age distribution: 0-1 418, 1-2 165, 2-3 125, 3-4 88, 4-5 62, 5-6 44, 6+ 98.

Year	0-1	1-2	2-3	3-4	4-5	5-6	6+	Total	% Juv.
(1)	Survival rate = 0.535								
	Reproduction rate = 1.8, 2.5, 3.0, 4.0/pair adults.								
0	418	165	125	88	62	44	98	1,000	41.8
1	224	223	88	66	47	33	75	756	29.6
2	171	119	119	47	35	25	58	574	29.7
3	129	91	64	64	25	19	44	436	29.5
4	110	69	49	34	34	13	34	343	32.0
5	86	59	37	26	18	18	25	269	31.9
(2)	Survival rate = 0.68								
	Reproduction rate = 1.8, 215, 3.0, 4.0/pair adults.								
0	418	165	125	88	62	44	98	1,000	41.8
1	284	284	112	85	59	42	96	962	29.5
2	277	193	193	76	57	40	94	930	29.7
3	265	188	131	131	51	39	91	896	29.5
4	289	180	128	89	89	35	89	899	32.1
5	287	196	122	87	60	60	84	896	32.0
6	282	195	133	83	59	41	98	891	31.6
7	278	191	133	91	56	40	95	884	31.4
8	274	189	130	90	61	38	92	874	31.1
9	272	186	128	88	61	42	89	866	31.4

Appendix VIII. (continued).

Year	0-1	1-2	2-3	3-4	4-5	5-6	6+	Total	% Juv.
10	270	185	127	87	60	41	89	859	31.4
11	268	184	126	86	59	41	89	853	31.4
12	266	182	125	85	58	40	88	844	31.5
13	264	181	124	85	58	39	87	838	31.5
14	261	179	123	84	57	39	86	829	31.4
15	259	177	122	83	57	39	85	822	31.5
16	257	176	120	83	56	39	85	816	31.4
(3)	Survival rate = 0.69								
	Reproduction rate = 1.8, 2.5, 3.0, 4.0/pair adults.								
0	418	165	125	88	62	44	98	1,000	41.8
1	288	288	113	86	60	42	97	974	29.5
2	285	199	199	78	59	41	97	958	29.7
3	277	196	137	137	54	41	95	937	29.5
4	306	191	135	94	94	37	94	951	32.1
5	309	211	132	93	65	65	91	966	31.9
6	307	213	146	91	64	45	107	973	31.5
7	305	211	146	100	62	44	104	972	31.3
8	307	211	146	101	69	43	102	979	31.3
9	309	211	145	100	69	47	100	981	31.4
10	311	213	146	100	69	48	102	989	31.4
11	314	215	147	100	69	48	104	997	31.4
12	314	216	148	101	69	47	104	999	31.4

Appendix VIII. (continued).

Year	0-1	1-2	2-3	3-4	4-5	5-6	6+	Total	% Juv.
13	316	217	149	102	69	47	105	1,005	31.4
(4)	Survival rate = 0.75								
	Reproduction rate = 1.8, 2.5, 3.0, 4.0/pair adults.								
0	418	165	125	88	62	44	98	1,000	41.8
1	314	313	123	93	66	46	106	1,061	29.5
2	337	235	235	92	70	49	114	1,132	29.7
3	356	252	176	176	69	52	123	1,204	29.5
4	428	267	189	132	132	52	131	1,331	32.1
5	470	321	200	142	99	99	138	1,463	32.1
(5)	Survival rate = 0.69								
	Reproduction rate varied in a three year cycle = 1.8, 2.5, 3.0, 4.0; 0.2, 1.8, 2.5, 3.0; 0.6, 2.4, 2.4, 3.0/pair adults.								
0	418	165	125	88	62	44	98	1,000	41.8
1	288	288	113	86	60	42	97	974	29.5
2	179	198	198	77	59	41	95	847	21.1
3	198	124	137	137	53	40	94	783	25.2
4	304	137	85	94	94	37	93	844	36.0
5	193	209	94	58	64	64	89	771	25.0
6	212	133	144	65	40	44	106	744	28.4
7	268	146	91	99	45	27	104	780	34.3
8	167	185	101	63	68	31	91	736	26.7
9	190	115	128	69	43	47	84	676	28.1

Appendix VIII. (continued).

Year	0-1	1-2	2-3	3-4	4-5	5-6	6+	Total	% Juv.
10	246	131	79	88	48	30	91	713	34.5
11	156	170	90	54	60	33	83	646	24.1
12	175	107	117	62	37	42	80	620	28.2
(6)	Survival rate = 0.70								
	Reproduction rate varied in a three year cycle = 1.8, 2.5, 3.0, 4.0; 0.2, 1.8, 2.5, 3.0; 0.6, 2.4, 2.4, 3.0/pair adults.								
0	418	165	125	88	62	44	98	1,000	41.8
1	293	292	115	87	61	43	99	990	29.5
2	187	205	204	80	61	43	99	879	21.2
3	209	131	143	143	56	42	100	824	25.3
4	325	146	91	100	100	39	100	901	36.0
5	209	227	102	64	70	70	97	839	24.9
6	234	146	159	71	44	49	117	820	28.5
7	300	163	102	111	50	31	116	873	34.3
8	189	210	114	72	78	35	103	801	23.5
9	219	132	147	80	50	54	97	779	28.1
10	288	153	92	103	56	35	106	833	34.5
(7)	Survival rate = 0.75								
	Reproduction rate varied in a three year cycle = 1.8, 2.5, 3.0, 4.0; 0.2, 1.8, 2.5, 3.0; 0.6, 2.4, 2.4, 3.0/pair adults.								
0	418	165	125	88	62	44	98	1,000	41.8

Appendix VIII. (continued).

Year	0-1	1-2	2-3	3-4	4-5	5-6	6+	Total	% Juv.
1	311	313	123	93	66	46	106	1,058	29.3
2	210	233	234	92	69	49	113	1,000	21.0
3	250	157	174	175	69	51	120	996	25.1
4	417	187	117	130	131	51	128	1,161	35.9
5	288	312	140	87	97	98	134	1,156	24.9
6	342	216	234	105	65	72	173	1,207	28.3
7	469	256	162	175	78	48	183	1,371	34.2
8	315	351	192	121	131	58	173	1,341	23.4
9	388	236	263	144	90	98	172	1,391	27.8

(8) Survival rate = 0.75 for first three year classes, 0.65 for final four;

Reproduction rate = 1.8, 2.5, 3.0. 4.0/pair adults.

Year	0-1	1-2	2-3	3-4	4-5	5-6	6+	Total	% Juv.
0	418	165	125	88	62	44	98	1,000	41.8
1	272	313	123	93	57	40	92	990	27.4
2	257	204	235	92	60	37	85	970	26.4
3	256	192	153	176	69	39	79	964	26.5
4	296	192	144	114	114	44	76	980	30.2
5	298	222	144	108	74	74	77	997	29.8
6	295	223	166	108	70	48	98	1,008	29.2
7	291	221	167	124	70	45	94	1,012	26.7
8	293	218	165	125	80	45	90	1,016	28.8
9	296	219	163	123	81	52	87	1,021	28.9
10	297	222	164	122	79	52	89	1,025	28.9

Appendix VIII. (continued).

Year	0-1	1-2	2-3	3-4	4-5	5-6	6+	Total	% Juv.
11	297	222	166	123	79	51	90	1,028	28.8
12	299	222	166	124	79	51	91	1,032	28.9
13	302	224	166	124	80	51	92	1,039	29.0
(9)	Survival rate = 0.75 for first three year classes, 0.65 for final four; Reproduction rate varied in a three year cycle = 1.8, 2.5, 3.0, 4.0; 0.2, 1.8, 2.5, 3.0; 0.6, 2.4, 2.4, 3.0/pair adults.								
0	418	165	125	88	62	44	98	1,000	41.8
1	272	313	123	93	57	40	92	990	27.4
2	162	204	235	92	60	37	86	876	18.4
3	178	121	153	176	60	39	80	807	22.0
4	295	133	91	114	114	39	77	863	34.1
5	182	221	100	68	74	74	76	795	22.8
6	203	136	165	75	44	48	97	768	26.4
7	254	152	102	124	48	28	95	803	31.6
8	153	191	114	76	80	31	80	725	21.1
9	181	114	143	86	49	52	73	698	25.9