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THERMAL ADAPTATION IN NORTH AMERICAN STURNIDAE

by

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ABSTRACT

Differential colonization success by the European starling (Sturnus vulgaris) and the tropical crested myna (Sturnus cristatellus), both introduced to North America in the late 1890's was examined in the Lower Mainland of British Columbia. Evidence existed which indicated mynas might be less well adapted than the European starling to the thermal regime in the Lower Mainland, thus, the following hypothesis was formulated: "an important reason for the observed difference in colonization success in North America by starlings and crested mynas is the relative difference in thermal adaptation".

To test the above hypothesis a two part study was designed. (1) Field measurements indicated nesting season, clutch size, hatching success, growth, fledging success and ontogeny of thermoregulation for both species. Also, simple field experiments were designed to measure incubation temperatures and determine results of between species cross-fostering studies. (2) Laboratory investigations were conducted on wild caught, captive adults. Energy input, outgo and metabolic response to temperature fluctuations were measured under both laboratory and outside Vancouver conditions for both species. Finally, plumage quality was assessed in a series of cooling experiments using feathered and unfeathered carcasses of both species.

The most important factors supporting my hypothesis were the relatively low nest attentiveness and consequent poor incubation success exhibited by crested mynas, compared with both the European starling living in the same environment and the common myna (Sturnus tristis) living in West Bengal (India).

Basal resting metabolism in both the crested myna and the European starling did not deviate significantly from the predicted values for birds of similar weight, however, at the extremes in the environmental temperature spectrum, both adult and nestling mynas were not as efficient in conserving energy as the starlings. Nestling myna growth (weight gain and plumage development) was slower than starling growth, however, nestling response to fluctuations were not different if comparisons are made on the basis of percent total plumage development.

The results of cooling experiments indicated that adult crested myna plumage was an inferior insulator against cold compared with starling plumage.

Results of bioenergetics investigations suggested mynas required more energy at colder temperatures to maintain a daily caged existence.

Poor correlations were observed between energy intake, energy metabolizable and energy excreted by caged birds and environmental temperature fluctuations in an outdoor

situation. Only in the colder than usual early half of 1969 was there significant correlations between metabolizable energy and environmental temperature.

Factors not investigated in this study were:

(1) inter and intra specific competition, (2) differential response to interference by humans, resulting in mortality, and (3) food limitations throughout the year which could limit sturnid populations in the Lower Mainland.

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INTRODUCTION

The sturnids or starlings and starling-like birds are native to Europe, Africa and Asia (Wetmore 1964). The family includes 100 species (Amadon 1946), two of which were introduced to North America in the late nineteenth century. First attempts to introduce starlings (Sturnus vulgaris vulgaris L.) in Pennsylvania in 1850 and in Ohio in the winter of 1872-73 failed (Phillips 1928). Later in 1889, 20 pairs were released in Portland, Oregon, and although the population initially increased, the colony presumably died out around 1901 or 1902 (Lord 1902). Finally, 40 pairs of starlings were successfully introduced in 1890 and 1891 at Central Park, New York City (Forbush 1915).

Within the last century, starlings have been successfully introduced to and subsequently spread in all continents except South America. Sturnus vulgaris originates from a temperate environment and most populations which breed in high latitudes migrate to warmer areas during cold months. Banding returns suggest that the majority of starlings breeding in the south coastal area of British Columbia are not migratory, while most birds breeding further north do migrate to and through the south coast of the province in the fall and spring. A similar situation exists in Britain (Thompson 1926). Barnes (1951) however, mentions that introduced starlings did not show migratory tendencies during

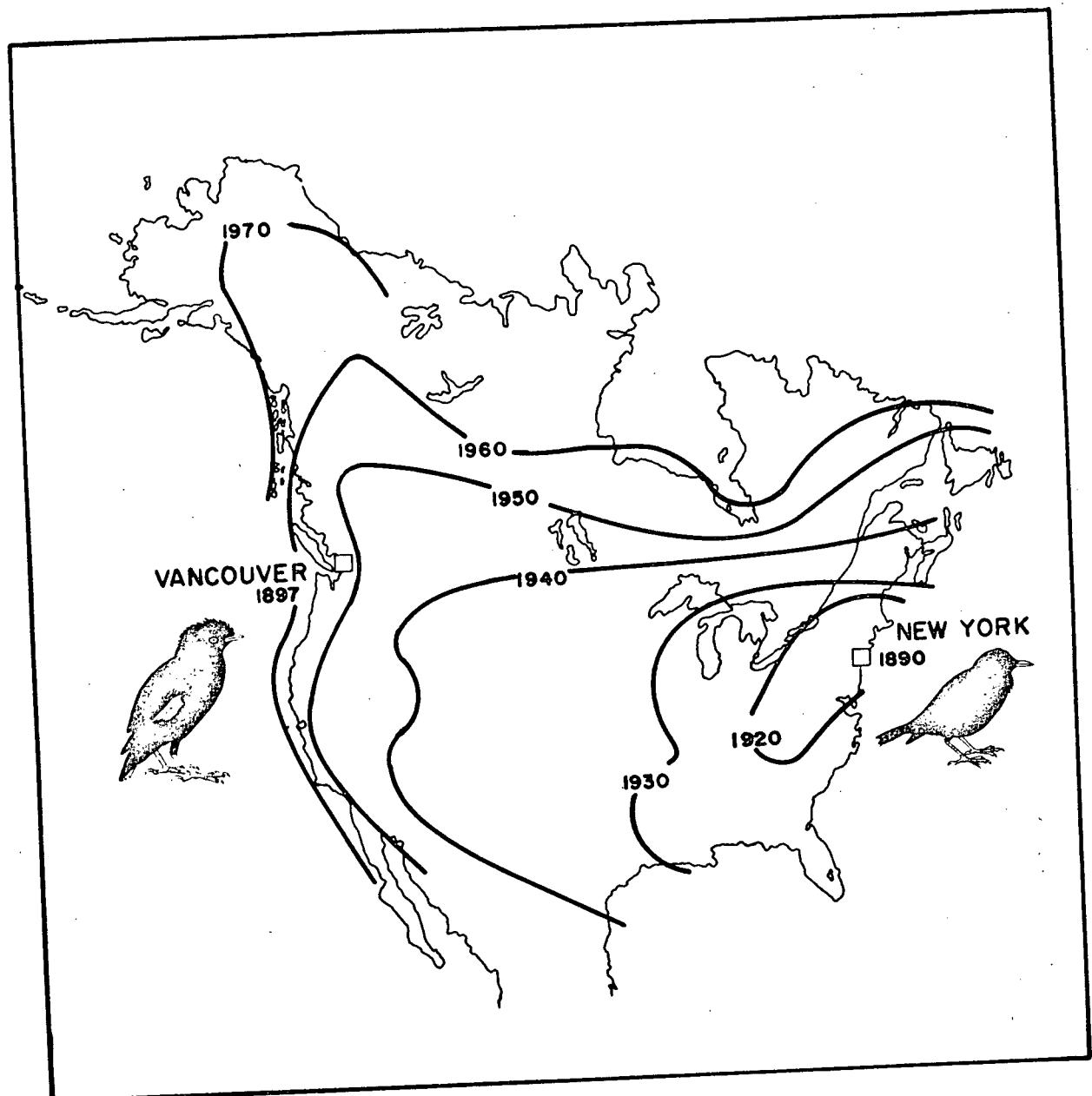
their first years in North America, but may have acquired the trait through association with blackbirds and other migratory species.

The crested myna (Sturnus cristatellus cristatellus (Deignan)), is a subtropical member of the Sturnidae, and was introduced to Vancouver, British Columbia, in 1897. Apparently only 1 or 2 pairs either escaped or were released to found the entire colony (Cummings 1925).

The taxonomy of the crested myna is unsettled. Deignan favours the genus Sturnus over Acridotheres (McClure, personal communication, 1969), while others cannot agree. Taxonomy following Deignan has been accepted in this study.

Earlier, the crested myna was successfully introduced to the Phillipines in 1850, however, egg collecting and shooting kept the population reduced (McGregor 1920). They have also been imported into Japan and Germany and sold as domestic pets for many years (Wood 1934:132). The crested myna is native to the subtropics of Southeast Asia including Southern China, Eastern India, Taiwan and the Indochinese region (Delacour and Mayr 1946; Ali 1949; Smythies 1953; Whistler 1949; Wildash 1968). Figure 1 illustrates the general patterns of colonization of both species since their respective introductions to North America in 1890 and 1897. Although the crested myna has not been as successful a

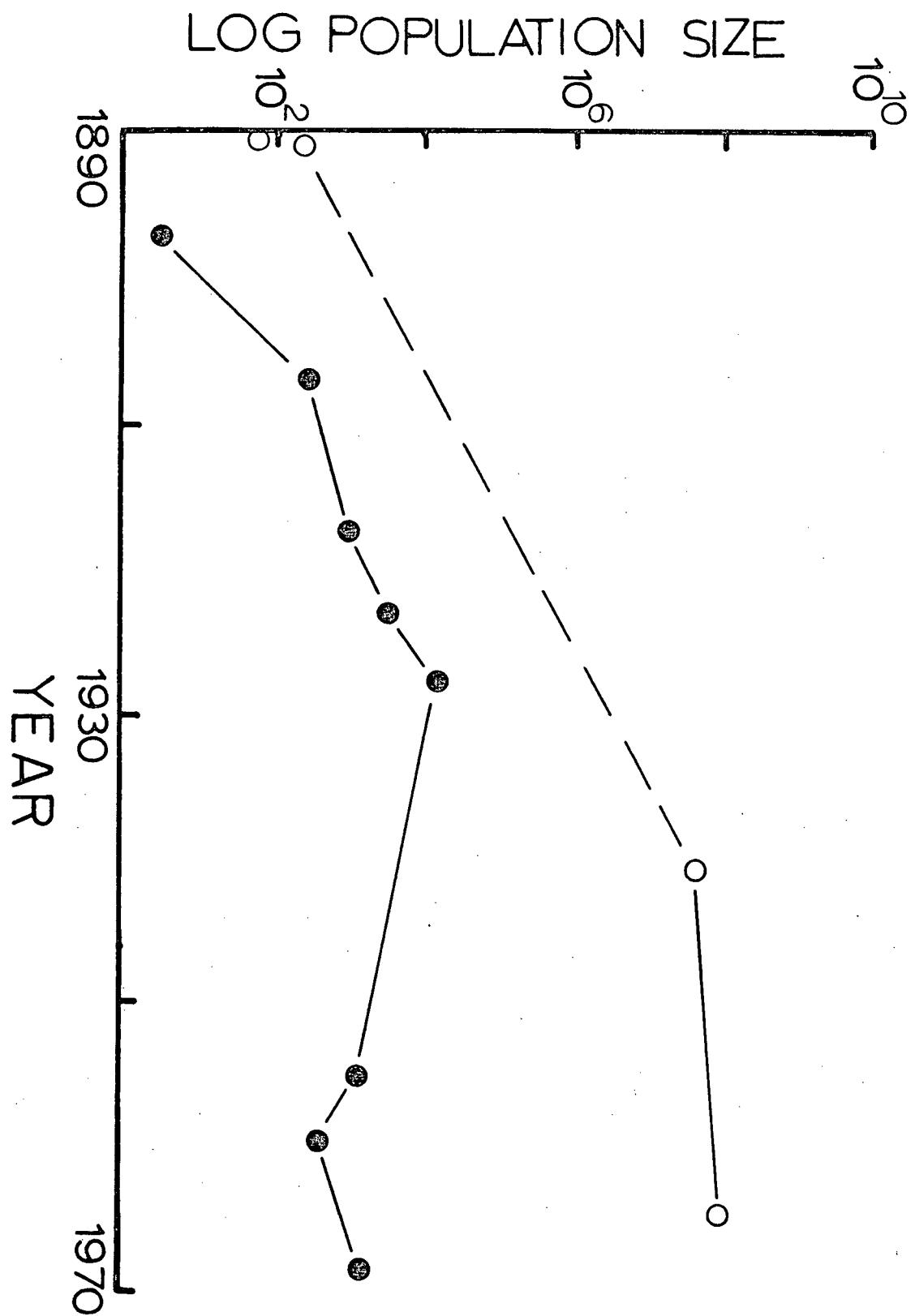
Figure 1. Isopleths designate extent of starling colonization since introduction at New York in 1890. No increase in myna distribution has occurred.



colonizer as the European starling, many early sources expressed alarm at the rate in which the myna population increased in the Vancouver area between 1897 and 1927 (Kermode 1921; Munro 1922; Racey 1924; Cummings 1932; Kelley 1927: See Figure 2). Early reports noted mynas seen near Blaine, Washington, (Cummings 1925) and as far south as Portland, Oregon, (Gabrielson and Jewett 1940) and Seattle, Washington, (Jewett et al 1953). Saunders (1930) reported crested mynas common at Alert Bay, British Columbia, however, Munro (1930) questioned this report. Crested mynas established themselves in Nanaimo, British Columbia, (Vancouver Island) in the early 1950's (Scheffer 1955), however, a breeding pair was shot in Victoria, British Columbia (Vancouver Island) as early as 1946. The myna population reached a peak in the late 1920's with numbers in British Columbia estimated at near 20,000 (Kelley 1927).

Scheffer (1931) noted that myna numbers had been stable for the 3-4 year period prior to 1931. Cummings (1932) reported mynas naturally decreasing during the early 1930's. Cowan estimated the population to be 4,000 birds in 1955 (Scheffer 1955). More recently, MacKay and Hughes (1963) estimated the myna population to be about 2000-3000 birds. The present population is probably near 5000-6000 birds (Figure 2).

Figure 2. Relative growth of myna and starling populations since their introductions in 1897 and 1890 at Vancouver and New York, respectively (o = starling; • = crested myna).



After a review of the relative colonizing success of these two sturnids, the obvious question arises as to the causes of such a difference. The myna is a non-migratory subtropical sturnid whose recent evolution has been in an environment quite different from the temperate regions of Europe and Western Asia, from which the European starling originates. Being non-migratory, only two other major avenues of colonization were open; dispersal from an overpopulated environment and/or wanderlust similar to that described for the European starling by Cooke (1928:3). Except for the earlier scattered sightings in Oregon and Washington, no accounts of crested myna sightings have been made outside the present restricted North American range of the species. Thus, the question is posed, why has the myna population not increased to the point where dispersal to other areas has become effective.

The hypothesis upon which this research was based is the following: an important reason for the observed difference in success of colonization by North American Sturnidae has been the relative difference in thermal adaptability.

A priori evidence exists for the formulation of such an hypothesis. Initiation of egg laying by mynas in North America and Asia begins at the same time; about 15 April (MacKay and Hughes 1963; Vaughn and Jones 1913). However,

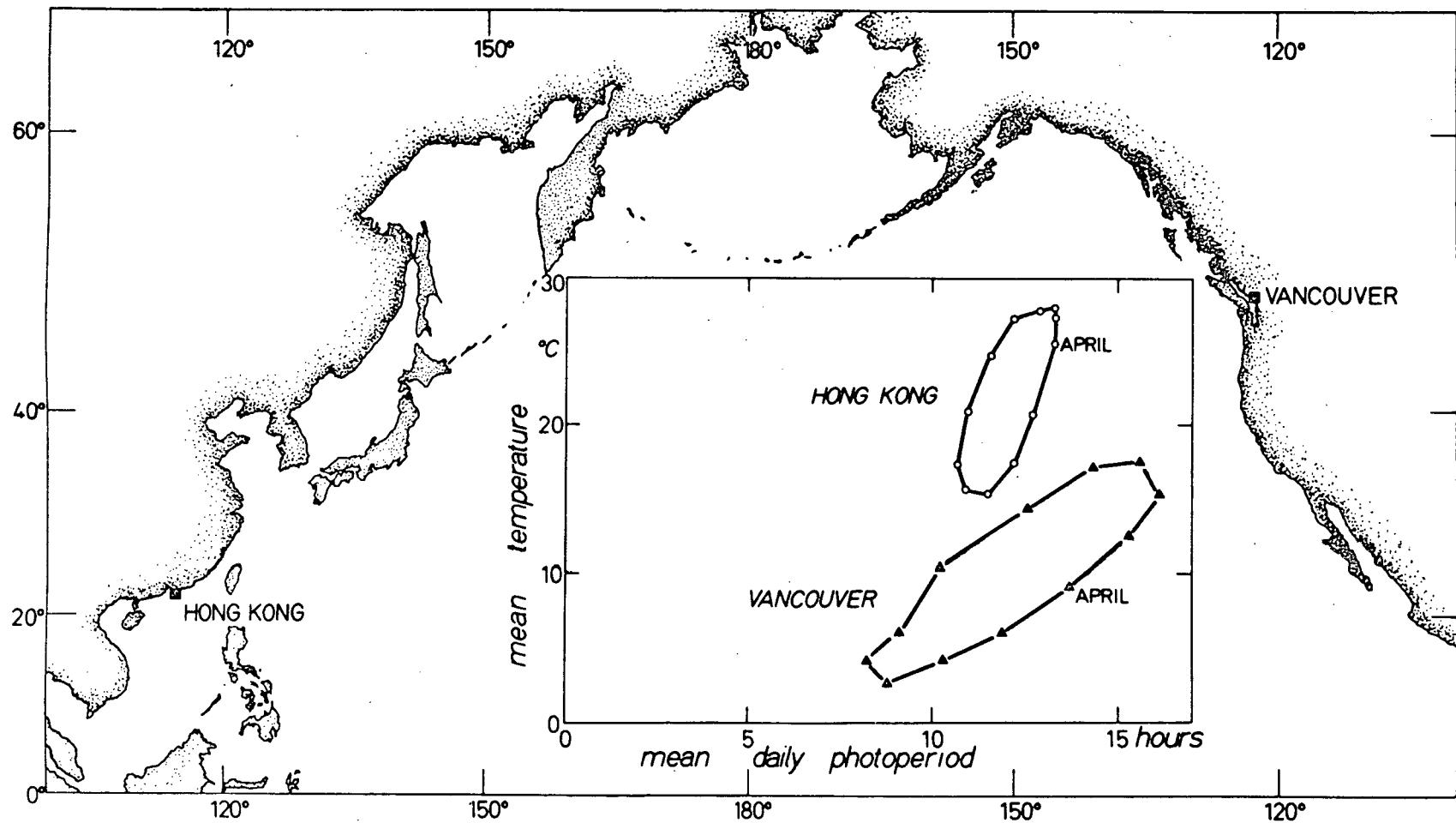
the mean 10-day daily temperature prior to egg laying for mynas is approximately 11°C lower in Vancouver (10°C) than in the Hong Kong and Macao area of South China (21°C) from which the birds were supposedly imported, and which is near the northern limit of the species' distribution. Figure 3 presents climographic illustration of the temperature and photoperiod regimes in Vancouver and Hong Kong.

Starlings, on the other hand, initiate egg laying at many different temperature and photoperiod combinations throughout Europe, North America, Britain and Western Asia (Kessel 1957; Royall 1966; Anderson 1961; Dunnet 1955; Havlin and Folk 1961).

Further, there is evidence that mynas suffer during cold weather. In Vancouver, observers have noticed mynas huddled on chimneys near heat effluent on cold winter days (Cummings 1925; Weber personal communication; and my own records). Philips (1928) also mentioned that mynas suffer from cold and would probably be confined to the immediate coast. There is no such evidence that starlings similarly suffer in cold climates, presumably because most populations migrate to warmer areas during winter.

In general, the ability of a species to withstand a broad range of the thermal spectrum is dependent upon its success in conserving energy. King and Farner (1960) have

Figure 3. Climograph showing mean temperature and photo-period in native myna habitat (Hong Kong) and introduced myna habitat (Vancouver). Data contributed by Canada Dept. of Transport, 1969, and the Royal Observatory, Hong Kong, 1969.



given a comprehensive review of energetics theory pertaining to birds. Tolerance to a particular environmental temperature range is the result of evolution and adaptation that has taken place in a particular type of environmental system. Scholander (1955 and 1956) has given a good discussion of temperature adaptation by both arctic and tropical species, and discusses the basic theory behind climatic adaptation in homeotherms.

After examining the above evidence, a two-part study was initiated to investigate sturnids in the lower mainland of British Columbia. Field data were collected to obtain basic natural history information on breeding biology, growth and development of young. Simple field experiments were designed to determine the rate, quantity and quality of energy intake by growing young and to determine the incubation success of adult sturnids. Laboratory investigations were made of the metabolic responses by adult sturnids to varying temperatures and to determine the relative insulation values of the plumage of both species. Adults of both species were captured and kept in outdoor aviaries under Vancouver climatic conditions where their bioenergetics were investigated.

MATERIALS AND METHODS

Field Studies

One hundred cedar nestboxes were constructed from the design described by Kessel (1957). These boxes were placed throughout the Vancouver area, with emphasis on locations near the University of British Columbia, and upon the islands of the Fraser River delta, which represent the major agricultural districts in that portion of the Puget Sounds Lowlands (See Cowan 1965:19-20) lying within British Columbia. Nestboxes were checked several times each week during nest building, egg laying, incubation and growth. During this study 4 active starling and 4 active myna nestboxes were equipped with Yellow Springs Instrument Co. (YSI) thermistor probes (#504) for monitoring nest temperature in the vicinity of the egg cluster. A YSI telethermometer was then used to check incubation temperatures during visits to the nestboxes. Also, 2 myna and 2 starling nestboxes were constantly monitored during incubation using Rustrak model 288, 2 channel temperature recorders. In addition to ambient and nestbox temperatures, core temperatures (proventricular) were recorded using an instant reading Schultes Reptile thermometer (-10°C to +50°C).

Most adult and all non-experimental nestlings were banded with U.S. Fish and Wildlife Service aluminum leg

bands. During growth, nestlings were marked with adhesive polyvinyl chloride tape (See Johnson 1971) for individual identification.

Oxygen consumption and change in core temperature were recorded for a series of developing starlings and mynas exposed to varying ambient temperatures in a Bellcraft controlled environment cabinet (temperature fluctuated $\pm 1.0^{\circ}\text{C}$). A Beckman F-3 paramagnetic analyzer was used to measure O_2 consumption from a closed system. Nestlings analyzed were not necessarily postabsorptive and R.Q. (respiratory quotients) determinations were not made. Body temperatures were recorded at the nest and again after they had been transported to the laboratory. Many starling nests were found within 200 yards of the laboratory and transport of these birds was easy, however, the closest myna nests (5 nests) were located 1 mile from the laboratory and heated insulated boxes were employed to insure against heat loss by these nestlings.

Growth was assessed by measurement of the longest primary as well as by weight gain. The latter was measured to the nearest 0.1 gm using Pesola #491 and 498 spring balances.

Feeding and activity rates of adult sturnids were ascertained by use of observers watching nestboxes through 30X spotting scopes. Continuous monitoring of the incubation

regimen and of the rate which adult sturnids feed their nestlings was undertaken by employing Licon model 10-722 microswitches attached to the top of nestbox holes, in conjunction with Esterline-Angus 20 channel event recorders.

Food items were collected from nestling starlings and mynas using the "close fitting collar" technique described by Kluijver (1933). Food items were then dried and subsequently analyzed for energy content using a Phillipson Micro-bomb calorimeter. Energy and weight values were pooled for calculating a daily mean energy intake of nestling sturnids.

In order to test differences in egg quality and in the effectiveness of incubation on the part of the two species, a series of interspecies crossfostering experiments were conducted in 1969 and 1970. In these experiments 5 myna and 5 starling clutches (5 eggs each) which were synchronized (\pm 1 day) in their incubation cycles were switched at day 2 from the nest of one species to the other and followed through incubation to hatching and fledging.

To investigate the role of nest temperature, 5 nest-boxes were modified using Electro-thermal heating tape and Fenwal #17300-23 thermal switches to keep nestbox temperatures from dropping below +28°C.

Captive adult starlings and mynas were obtained from wild populations in the Vancouver area in 1968-69. Starlings

were captured on the campus of the University of British Columbia using baited funnel traps. Crested mynas were captured with mist nets at night in a communal roost. Sex of starlings can be determined externally (Kessel 1951), and an even number of males and females were selected. Crested mynas, however, show no external sexual characteristics, therefore birds could not be collected on the basis of sex. No experimentation or data collection was initiated until the weight and behaviour of the birds indicated they had become adjusted to confinement (1-3 months).

Captive Studies

Initially, twenty birds of each species were captured and confined two per cage. Since competition for food and space within individual cages was evident, sample sizes were halved to one bird per cage. Experimental birds were housed in 0.5 x 1 x 1 meter cages outdoors at the Vivarium, University of British Columbia, where they were exposed to Vancouver temperature and light conditions. However, a roof over and opaque polyethylene sheeting around the cage area gave shelter from precipitation and wind. The moderating influence of this shelter on air temperature is shown in Appendix Table 1.

Food and water were available on an ad libitum basis from specially constructed containers designed to reduce spillage. All experimental birds were fed Buckerfield's Chick Starter with Amprolium crumbles (anticoccidiosus agent). Buckerfield's guarantees the following analysis of their Chick Starter:

(Min.) Protein	(Max.) Fat	(Max.) Fiber	NaCl	P	(Min./lb) Vit. A	Amprolium
20%	3.5%	5.5%	0.45%	0.7%	1500 I.U.	0.0125%

Energy utilization experiments were conducted for the year period 1 January 1969 to 1 January 1970. Feed cans were weighed before and after each trial and filled with fresh feed every two days. Water was also changed every two days except in winter when freezing temperatures necessitated changing water every day.

Each 100 pound lot of feed purchased was subsampled and analyzed for energy content. Four energy determinations were performed for each feed subsample on a Gallenkamp adiabatic oxygen bomb calorimeter. The mean energy content of food was $4.53 \pm .01$ kcal/gm for eight 100 pound lots.

Two perches were placed in each cage from which birds excreted onto non-absorbent paper unrolled beneath each row of cages. The paper was pulled from the ends of cage rows

and the excreta were collected for each cage on sections cut from the roll. Excreta collections were made over 2-8 day periods throughout the year. Twenty-three collections were made during this study, representing 102 days of sampling.

Excreta were dried at 32°C in a steam-heated drying room for at least 7 days, after which the dried samples were scraped from the paper and placed in plastic bags. Excreta collections were later weighed, subsampled and analyzed twice for energy content. After drying was complete, feathers and spilled food were separated from excreta.

Weight of the experimental birds was measured twice per month and cage area ambient temperatures were measured every two days on maximum-minimum thermometers.

Bioenergetics data for captive sturnids were processed on an IBM 1130 computing system. Plotted graphs of some raw data are presented in Appendix Figure 1. For ease in statistical treatment, data were pooled into monthly means and an analysis of variance was run on an IBM 360 computing system. A value of $\alpha=0.10$ was chosen for all tests of significance.

Energy metabolism experiments were conducted on post-absorptive adult birds at night in a Bellcraft controlled environment cabinet (temperature fluctuations = $\pm 1.0^{\circ}\text{C}$). A closed system technique was used in which birds were placed on a perch in a 0.8 meter³ plexiglas box within the darkened

environment cabinet. Relative humidity in the respiration chamber was kept near 20% during experiments. Air temperatures were monitored using a YSI telethermometer with YSI # 401 probes. Oxygen utilization was measured with a Beckman F-3 Paramagnetic Oxygen analyzer (flow rate=250 cc/min); ascarite tubes were employed to analyze CO₂ from air samples withdrawn from the closed system. Birds were weighed and core (proventricular) temperatures were taken orally before and after metabolism experiments.

Trials were performed on birds of both species at ambient temperatures of -20°C through +40°C. Trials were conducted for 3 hours except at +20°C where trials lasted from 6-9 hours.

Postabsorptive state was assumed from determinations of rate of passage. This rate was determined by the use of food marked with carmine dye.

Experiments to determine insulative values for adult plumage of both species were conducted on fresh specimens in the environmental cabinet. Five starlings and four mynas were killed and immediately suspended by the beak in the cabinet and allowed to cool.

The rate of natural body heat loss was recorded with a YSI model 524 needle probe inserted into the carcass core during cooling experiments. Several birds were artificially

reheated to natural core temperatures and cooled again to test for possible differences between the loss of artificially induced and natural heat. Finally, the feathered carcass was again artificially reheated and feathers quickly stripped off, the carcass reheated the last few degrees to normal core temperature, and then allowed to cool without feathers.

Surface areas of defeathered bird carcasses were determined by covering the carcass with a thin layer of Dow-Corning Silicone Sealant. The sealant was allowed to cure and was removed in a manner similar to skinning. The carcass mold was then cut into sections, pinned out flat and traced. A polar planimeter was employed to determine the surface area of the tracing. Surface area data obtained in this manner were compared with those calculated using the formula of Meeh (1897: $S.A.=kw^{2/3}$) and the constant (k) obtained by Rubner (1902: $k=10.4$).

RESULTS

Nesting

The Starling

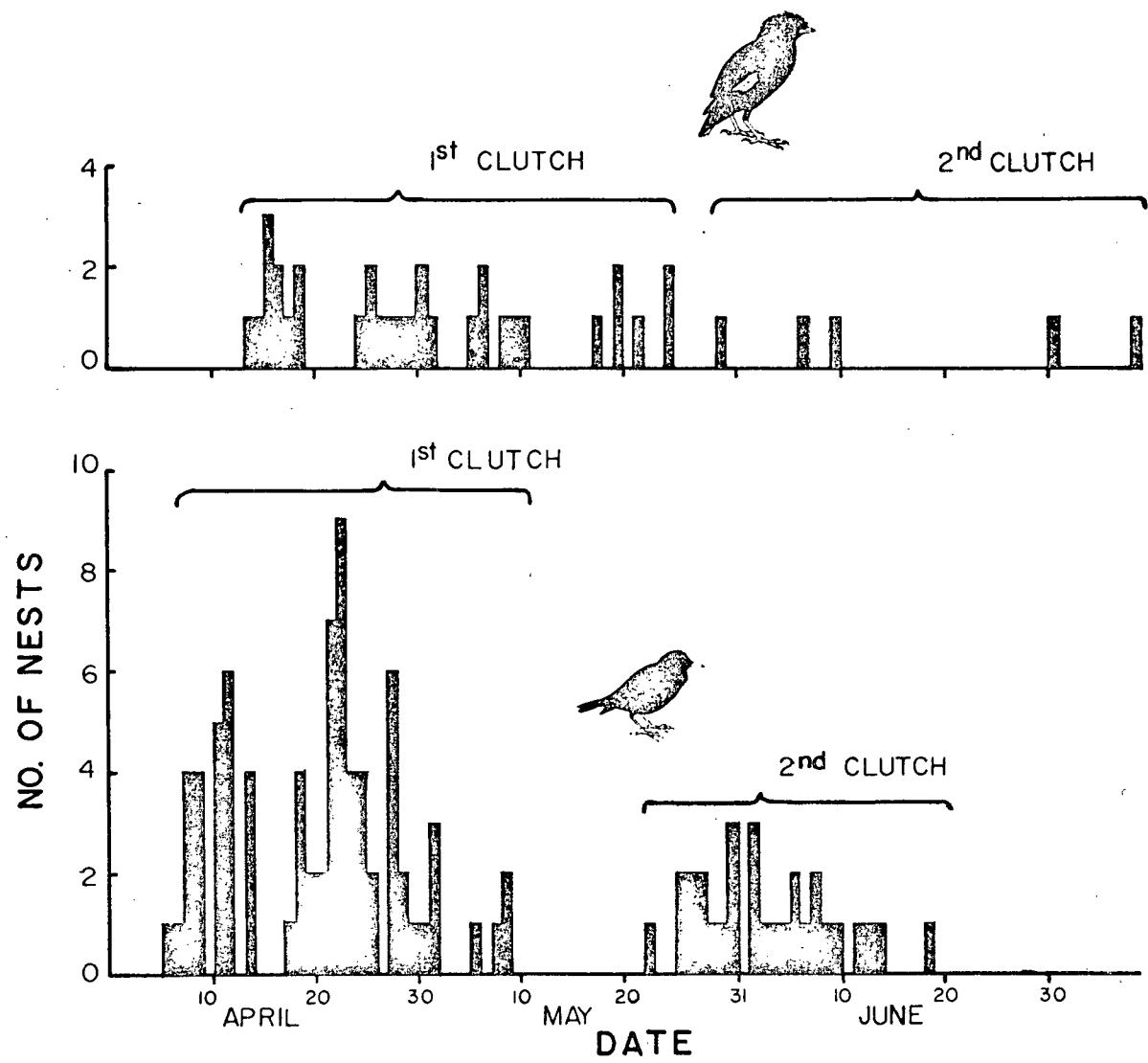
Nest building by starlings in the Vancouver area began in the second or third week in March. First eggs were usually laid in the second week of April, however, during 1970, starlings began nesting earlier and first eggs were laid in the first week of April (See Figure 4). The mean clutch size for all first nestings was $5.45 \pm .12$ eggs ($n=76$). Starlings are not strongly nest site tenacious, but 8 females did occupy the same box for two consecutive years. Thirty-nine percent of all starlings in this study successfully nested twice. These second clutches were started in late May with the peak of egg laying near 1 June, and exclusive of renestings they averaged $4.73 \pm .30$ eggs ($n=32$).

The Myna

The first myna nesting activity began in the second or third week of March. Males perched near the prospective nest site and vocalized loudly. In most cases mynas seemed already paired when nesting activity was initiated. Pairing probably occurred in the roost or away from the nest in late winter or early spring.

Older mynas are strongly nest site tenacious, with some nests occupied by at least 1 member of the same pair for the three year study period. Mynas are very aggressive birds

Figure 4. Dates of first eggs in first and second clutches for Vancouver Sturnidae.



and readily kill any nestlings and drive off parent birds of other species which establish themselves in a prospective myna nest. Myna nests are truly traditional; we were informed that one nest had been occupied by breeding pairs for over thirty years. These older nests were quite large and gaudy with bright papers, nylon stockings, plastic bags, balloons, bright feathers, mummified goldfinch and swallow carcasses, recorder tape and candy wrappers protruding from the nest hole.

Few mynas accepted any experimental nestboxes the first summer (1968) of this study, but more established themselves in these boxes during 1969 and 1970. By placing a cedar nestbox over the entrance to an established myna nest, mynas would nest in the boxes, thereby making their activities easier to monitor.

Mynas lay 1 egg/day with the mean for all first clutches $4.85 \pm .80$ eggs/clutch ($n=31$). First eggs were found from the second week of April, with no major peak in egg laying observed. First eggs/nest were still being found in late May when starlings were starting second clutches. Only five positive second nestings (exclusive of renestings) were observed in the three year study and these were scattered from late May through early August (Figure 4), and they averaged $3.83 \pm .47$ eggs.

Incubation

The Starling

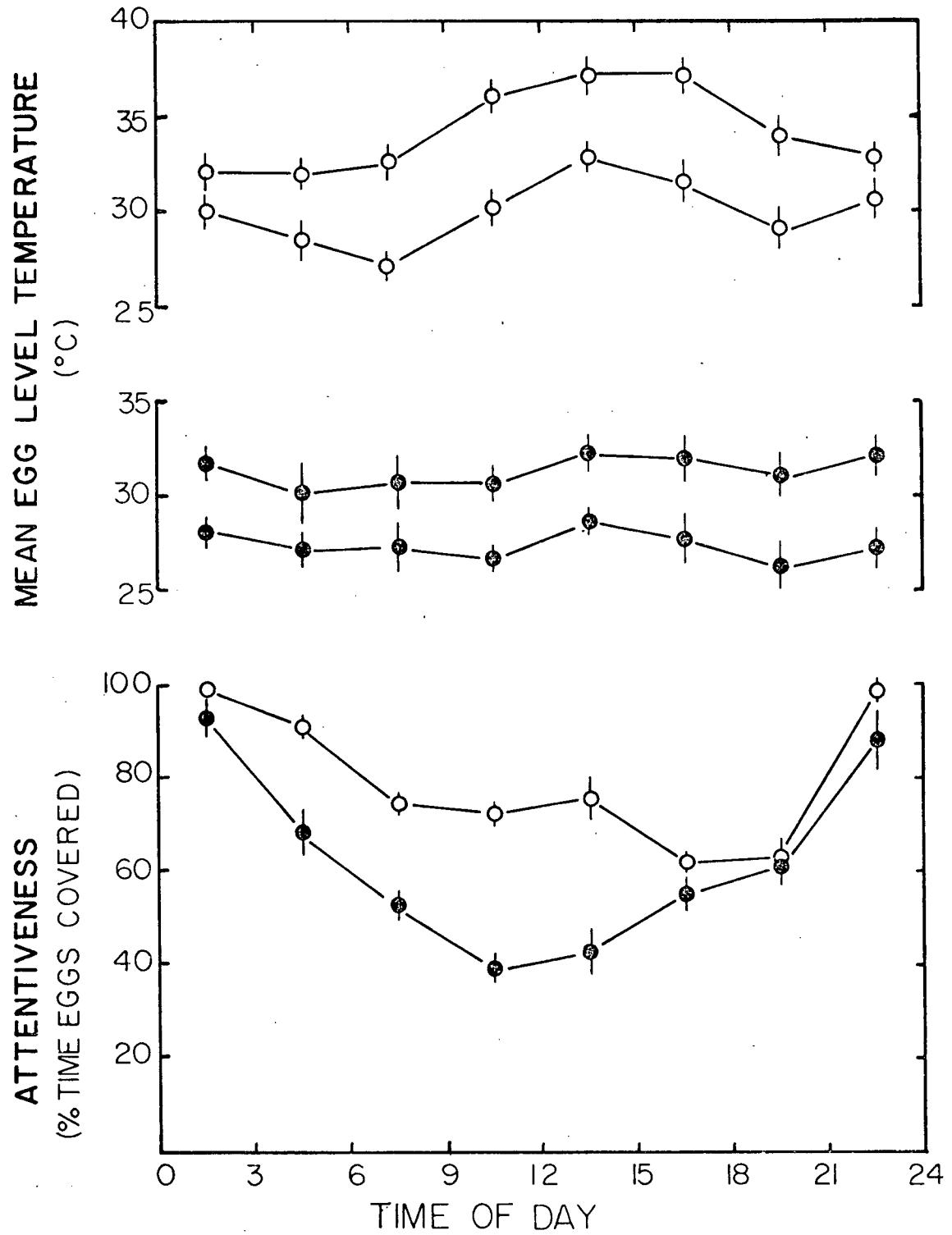
Pairs roosted away from the nest and continued to roost in communal roosts until incubation began after the last egg was laid. Both sexes incubated during the day, but only females at night. Some males flew to a distant communal roost at night during the incubation period, while others roosted singly near the nest.

Incubation in starlings lasted from 10-13 days, with 11 and 12 days most common. Actual incubation temperatures were not monitored but the temperature in the egg cluster averaged 33.0°C for starlings (Figure 5) with a mean daily nest attentiveness (% time eggs covered) of 77% (n=4 nests; 13 days) for first broods (70% during daylight period; 0300-2100). The maximum number of eggs successfully incubated was 7 of a clutch of 9.

The Myna

Incubation began after the last egg was laid, and both sexes incubated during the day. Sexing mynas in the field was almost impossible and too much tampering with incubating adults always resulted in nest desertion, therefore it was not ascertained which of the pair took most of the responsibility for incubation. The bird not incubating usually

Figure 5. Nest attentiveness and mean (\pm s.e.) daily maximum and minimum temperature in the egg cluster of Vancouver Sturnidae for the complete incubation period (o = starling; • = crested myna).



roosted near the nest at night. Incubation in mynas lasted from 12-15 days with 14 days most common. As with starlings, actual egg temperatures during incubation were not monitored but temperature in the egg cluster during incubation averaged 29.6°C (Figure 5) with a mean attentiveness (% time eggs covered) of 59% over the whole 24 hour period and 47% during the daylight period (n=4 nests; 14 days). The maximum number of eggs successfully incubated was 5 of a clutch of 6.

Hatching and Fledging

The Starling - Hatching

Hatching success should be defined as that percent of all eggs that survived in the nest at least as long as the normal incubation period. Failure to hatch was attributed to parental causes, infertile eggs, cracked eggs and predation:

	Undetermined Causes %	Parental Causes %	Infertile Eggs %	Cracked Eggs %	Predation %
Crested Myna(39%): ²	4	70	12	11	3
Starling(16%) ²	3	5	83	8	1

The majority of all predation was by humans (mostly children) however, crested mynas readily evicted any other birds attempting to occupy a traditional myna nest. In general, predation was low and as Ricklefs (1969a) has shown,

¹ Parental Causes includes desertion and chilling of eggs

² Percent of all eggs which did not hatch

the predation component of egg and nestling mortality is low for hole or cavity nesters.

Starlings hatched 84% of all eggs laid as first clutches (76 nests) during this study and a 69% hatching success was observed for second clutches (32 nests). From the time shells were pipped to complete escape from the egg sometimes took 24 hours, but usually only 8-10 hours was required. The mean weight of nestlings immediately after hatching was $5.7 \pm .81$ gms (18 observations).

Hatchling sturnids are typical altricial nestlings (ectothermic), and core temperatures (proventricular) at hatching varied (34.2 to 40.2°C) with the nest temperature and amount of brooding during hatching. Starlings hatched with long strands of down (1.0-1.5 cm) present on the capital, femoral and spinal pteryiae and with shorter down (0.25-0.50 cm) found on the alar and humeral pteryiae.

Nestling Mortality Factors

Nestling mortality was attributed almost solely to desertion (starvation and exposure), however, severe mite infestations in localized nest sites resulted in some nestling losses, and wounds inflicted by parent birds also resulted in a few losses. Adult sturnids promptly remove dead nestlings from the nest and detailed analyses of carcasses was impossible in most cases

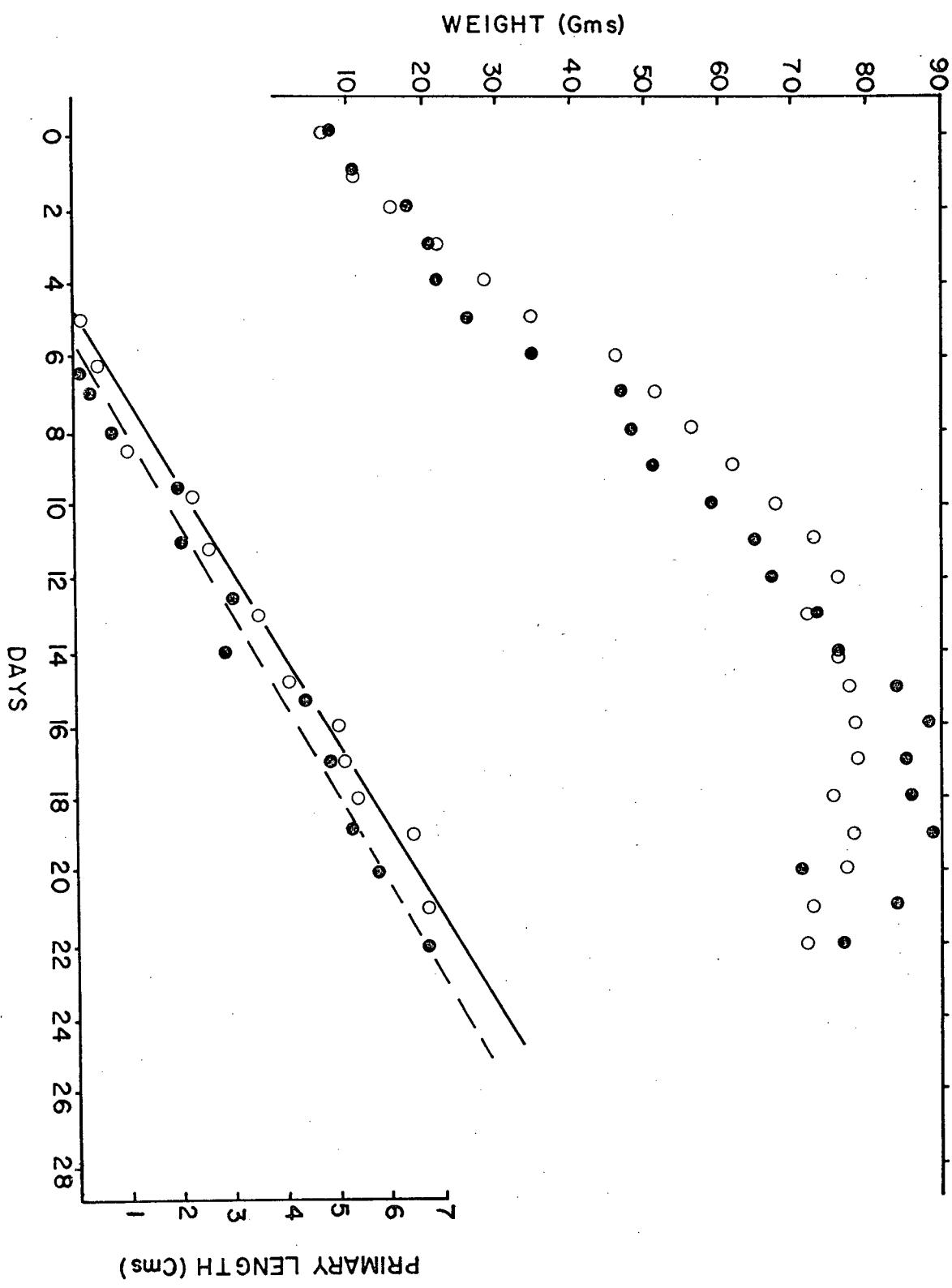
Fledging

Seventy-one percent of all eggs in first clutches laid by starlings eventually fledged; a 68% success was observed for eggs in second clutches. Just prior to fledging, the mean nestling weight decreased (Figure 6) as a result of reduced caloric intake, increased activity, and because some of the heavier nestlings fledged early. Adult feedings/nestling-hr decreased dramatically just prior to fledging and young birds became very active around days 19-21. Nestlings fluttered up to the nest hole and were commonly seen with head and breast out of the box. This increased activity by nestlings influenced the activity recordings, therefore after day 19, event recordings were not truly representative of adult feedings (Figure 10) and to obtain this information actual feedings were observed at different times of the day (after day 18) with a spotting scope.

Nest Parasitism

Many times fledgling starlings from other nests parasitized nest cavities already occupied by less developed nestlings. In one such case, a nest parasite was found to be an abandoned late hatching individual in a late stage of development from a nearby nestbox. In some instances these nest parasites actually consumed the majority of food brought by the parent birds, which resulted in death of the original brood.

Figure 6. Growth and plumage development of nestling Vancouver Sturnidae (\circ = starling; \bullet = crested myna).



For several days after leaving the nestbox, juvenile starlings are fed by parent birds in the field, and the majority of nest parasites are thought to be these fledged juveniles who became separated from their parents and returned to any active nestbox for parental care. Nest parasitism of this type was not uncommon; 28 different instances were observed during the 3-year study period.

After juvenile starlings became self-sufficient, they gathered into small flocks which first became evident in the Vancouver area in late June, when second clutches were hatching. As the summer progressed these sub-adult flocks congregated and enlarged, until late July or early August when the second broods fledged and joined them. The flocks continued to enlarge with the addition of adult birds. During this flock formation period the molt occurred and significant numbers of birds resumed use of communal roosting areas. With the coming of fall and lower temperatures, local flocks and communal roosts enlarged again with the influx of migrant birds from the interior of British Columbia. Peak numbers of starlings probably occurred from mid-September to mid-October; later the numbers began to decrease as the migrants continued their journey South.

The Myna - Hatching

Mynas hatched 61% of all eggs laid as first clutches (32 nests) during the three years of study, and a 58% hatching success was observed for 5 second clutches.

Hatching usually took 8-10 hours; the mean nestling weight immediately after hatching was $5.92 \pm .42$ gms (11 observations).

Mynas hatch with short down (0.25-0.50 cms) on the capital, spinal, femoral, alar and humeral pterylae. Hatchling mynas look very similar to starlings except that the cranium appears less rounded than starlings, the skin is pigmented more heavily giving the nestling a "suntanned" appearance, and the down is shorter.

Fledging

Nestling mynas were not as active as nestling starlings prior to fledging, however, increased activity still influenced activity recordings (Figure 10) and necessitated direct observations of nests during the late stages of nestling development. Young birds fledged near day 22 and flew to nearby trees or tall shrubs where they were fed by parent birds. Mynas formed strong family bonds and family groups were still seen in late fall. While leaves and fruit remained on deciduous trees, mynas congregated into local

communal roosts, but when the leaves and fruit dropped, these birds left and joined larger communal roosts with starlings and other mynas.

Forty-six percent of myna eggs in first clutches produced young that eventually fledged and 35% of the eggs from the five second clutches produced young that fledged.

Growth and Development

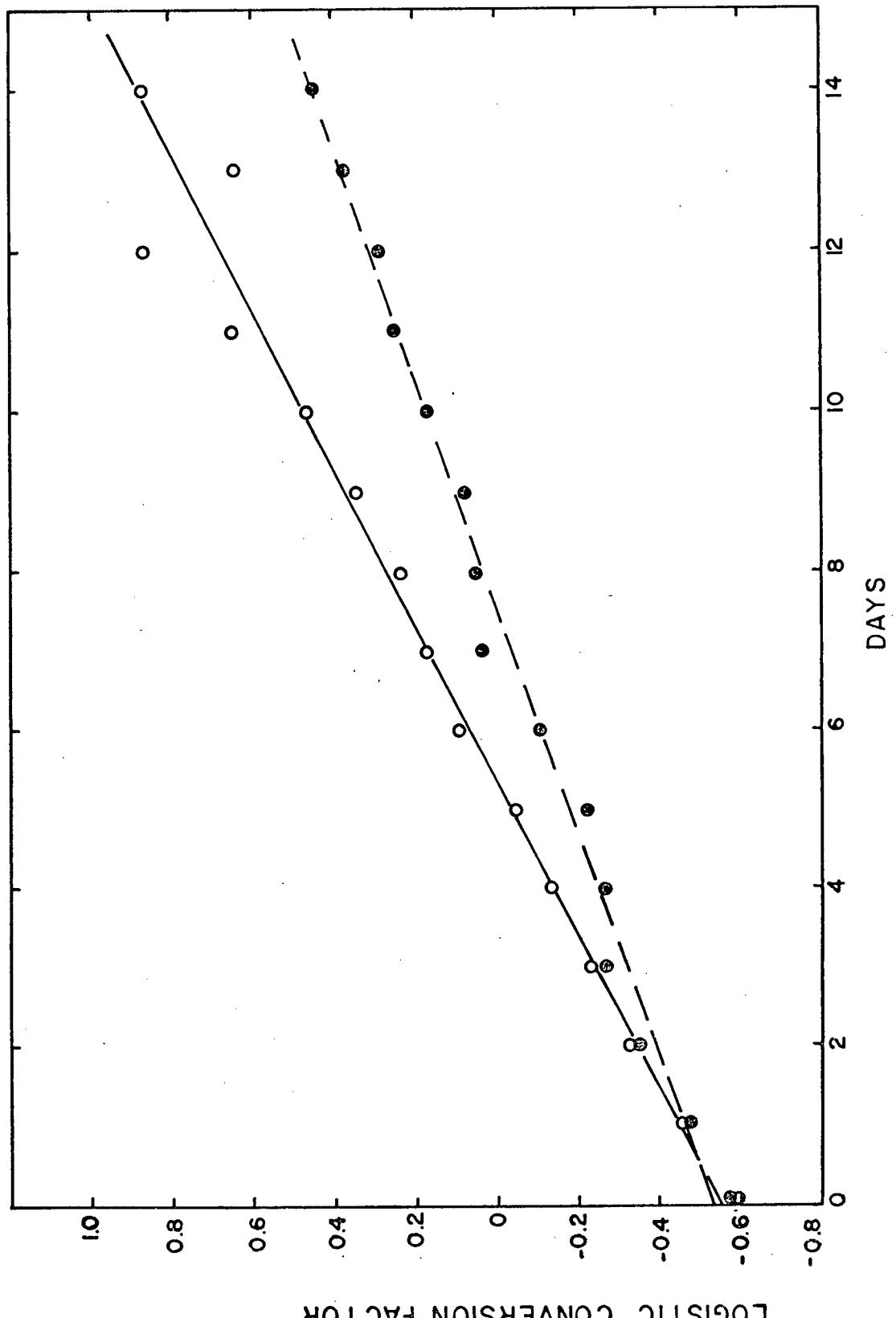
The Starling - Growth

Starling growth follows a sigmoid curve (Figure 6) described by the logistic equation: $W = \frac{78.56}{1 + e^{-0.416(t-5.3)}}$

where W is weight in gms; 0.416 is the growth rate constant (K); 5.3 (days) is the point of inflection of the curve; and 78.56 gms is the asymptotic weight. Figure 7 illustrates sturnid growth using the method described by Ricklefs (1967).

Development of flight feathers, although not exactly synchronized with total contour feather development, is a handy index of plumage development. Figure 6 also expresses the mean length of the longest primary on the right wing of growing nestling starlings. The pattern of feather growth, expressed as length of a single feather follows an arith-

Figure 7. Growth of nestling Vancouver Sturnidae,
presented in the manner described by Ricklefs
(1967) (\circ = starling; \ominus = crested myna).



metic increase, however, if weight of all the developing plumage were plotted against days, a geometric increase, similar to body weight, would probably be demonstrated.

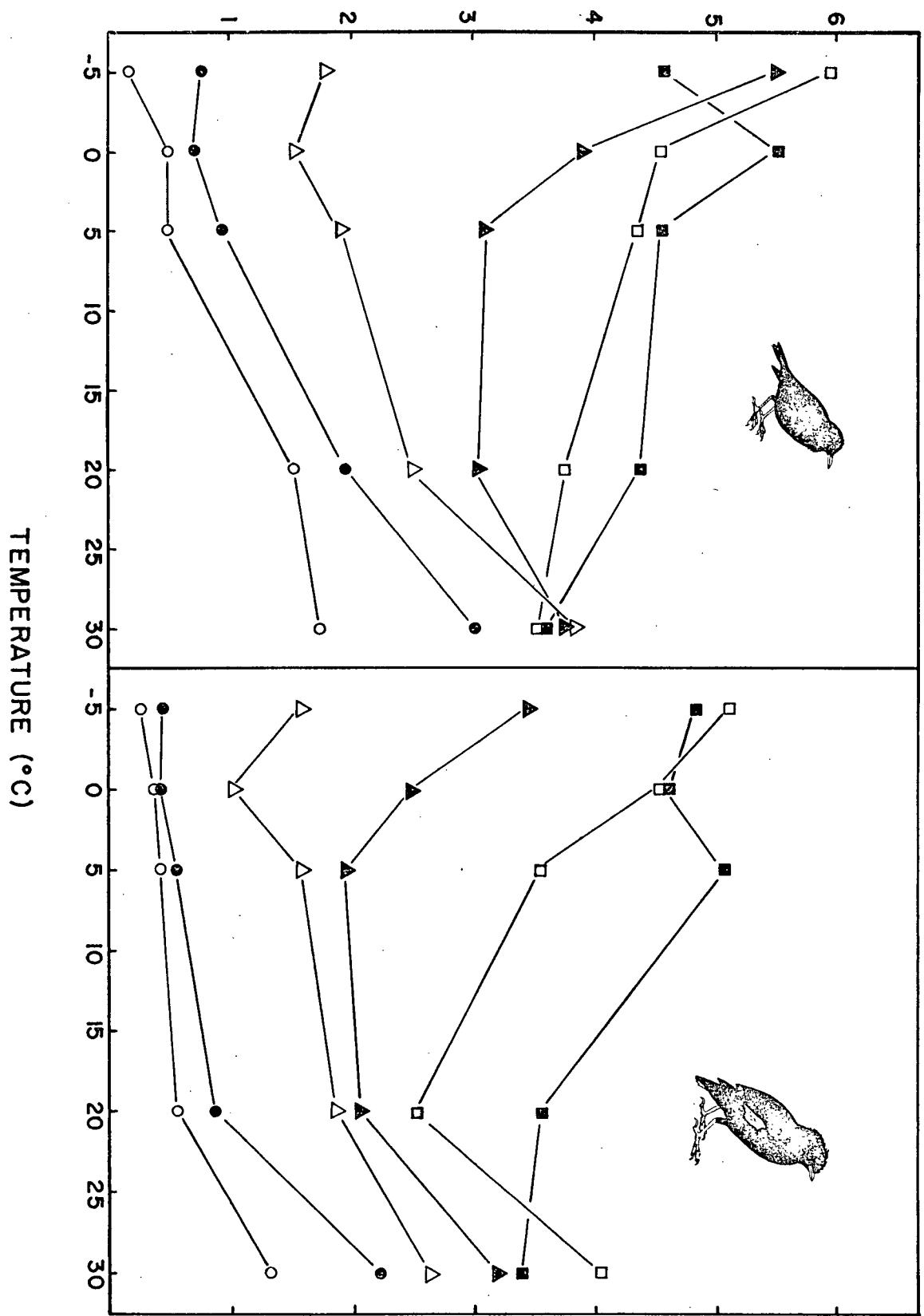
The entire clutch of eggs usually hatched the same day and weights of all the nestlings increased similarly during growth. Occasionally one egg hatched before or after the rest in which case that nestling always had a clear advantage or disadvantage with respect to growth or survival, depending on the total brood size. The bodies of nestling starlings were not completely covered with feathers until day 13 or 14; feather elongation was still taking place when the birds left the nest. Juvenile starlings molted their dull grey-brown plumage from late July (first broods) through early October, with some juvenile feathers still found on the capital and spinal tract in late December.

Development of Endothermy and Homeothermy

Nestling starlings were truly poikilothermic until days 13-15 after hatching. Figure 8 shows the development of endothermy in growing sturnids of different weight classes. Nestling starlings do not show a sustained heat production until feathers were almost fully developed (60-70 gms) and able to trap heat produced by the increase in metabolic

Figure 8. Development of internal heat production (endothermy) in nestling Vancouver Sturnidae; oxygen consumption at varying ambient temperatures by birds in different weight classes (\circ , \bullet , Δ , \blacktriangle , \square , \blacksquare , represent birds weighing between 10-20, 20-30, 30-40, 40-50, 50-60 and 60-70 gms, respectively).

OXYGEN CONSUMPTION (cc O₂ /gm-hr)



activity. Although heat production increased in the 60-70 gm nestling weight class, complete homeothermy was not attained until birds had almost reached asymptotic weights (Figure 9). Nestling starlings withstood amazingly extreme decreases in body temperature. All individuals tested at -5°C for 30 minutes survived, and one newly hatched starling (6.6 gms) survived extreme hypothermy ($t_b = 2.8^{\circ}\text{C}$) for 20 minutes, after which time it was re-heated to $+34^{\circ}\text{C}$ and replaced in its nestbox to eventually fledge.

Nestling Food Intake

During the growth period, the rate of food intake of nestlings increased, as is illustrated by the increase in activity (Figure 10) at two nestboxes (1 in 1969 and 1 in 1970) during incubation and growth. From hatching until about day 10, a steady increase in visits to the nest was monitored. From observing nestboxes with a 30X spotting scope, approximately 90% (91.6%) of all trips by both parents to the nest box resulted in an actual feeding. Applying this value to Figure 10 we arrive at an initial feeding rate of 2.5 to 3.0 feeding/nestling hour (18 hour feeding day) at hatching day (day 0) up to 8.0 feedings/nestling-hour at days 10-12 (18 hour feeding day).

Figure 9. Development of homeothermy in nestling Vancouver Sturnidae expressed as the change in body temperature (during 30 minute trials at - 5°C) of nestlings at varying stages of development (o = starling; • = crested myna)

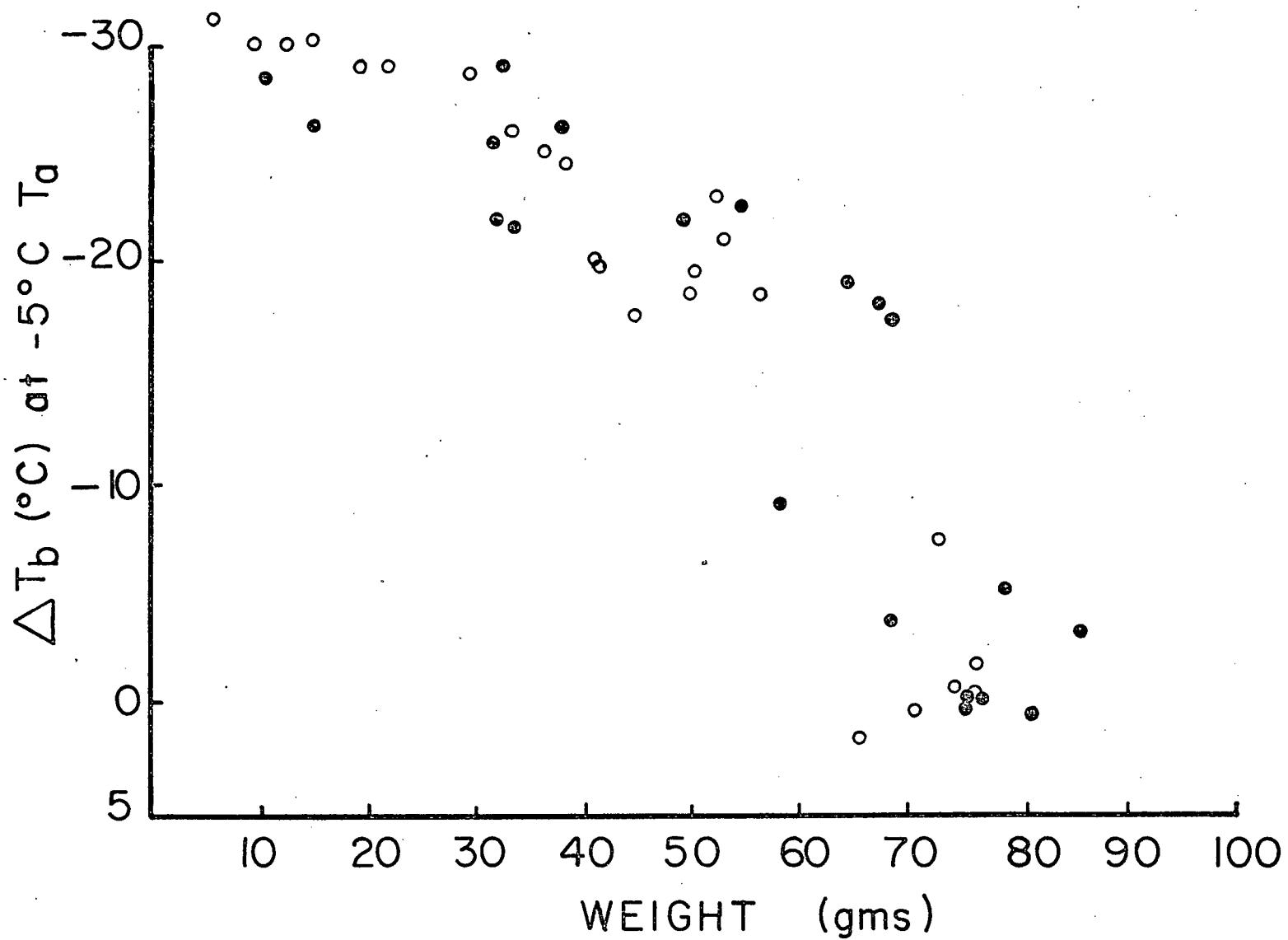
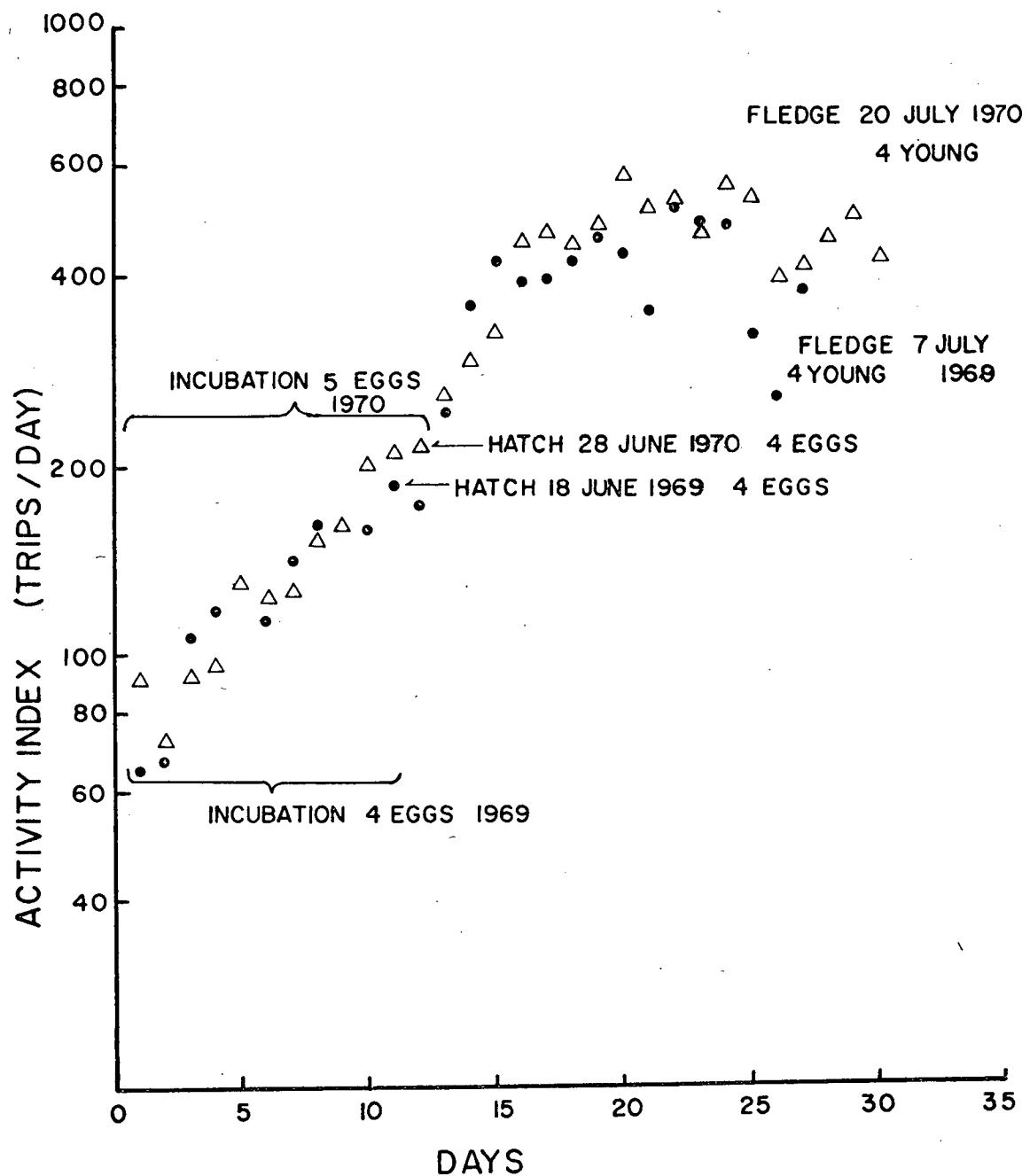


Figure 10. Adult activity at 2 starling (1 in 1969 and 1 in 1970) nestboxes.



The mean caloric value of food items collected from nestling starlings was $5.18 \pm .09$ kcal/gm (39 samples); a mean dry weight of $0.112 \pm .019$ gms/ feeding was observed for those same food items. Sample sizes were small in any one weight or age class, therefore data were pooled to obtain mean values. These values can similarly be applied to Figure 10 with the resulting description of gross energy intake (G.E.) of nestling starlings. G.E. intake increased from 1.45 kcal/nestling-hour (26.10 kcal/nestling-day) at hatching day up to 4.64 kcal/nestling-hour (83.52 kcal/nestling-day) at day 10-12.

There were differences in food items of nestling starlings depending upon location of the nest and time of year. If the nest was located near fruit trees late in summer, fruit (especially cherries and berries) contributed greatly to the diet of growing birds. Most first broods, however, were fed primarily animal matter, and regardless of the time of the year, very young nestlings (up to 5-6 days old) were fed almost exclusively animal matter (high protein). The mean caloric value of starling food items represents samples of both animal and plant food, therefore it may not be representative of caloric intake of late broods fed almost exclusively cherries past day 5-6.

The Myna - Growth

Myna growth follows a sigmoid curve (Figure 6) described by the logistic equation: $W = \frac{88.59}{1 + e^{-0.284(t-7.5)}}$

where W is weight in gms; 0.284 is the growth rate constant (K); 7.5 (days) is the point of inflection of the growth curve; 88.59 gms is the asymptotic weight. Figure 7 represents both starling and myna growth using the method described by Ricklefs (1967). Figure 6 expresses growth of myna plumage using length of the longest primary as an index of total feather development. As with starlings, myna eggs usually hatch on the same day, with weights of all nestlings increasing similarly during growth. However, if an egg hatched more than 1 day after the rest of the clutch, that nestling usually died, depending upon the total brood size.

The bodies of nestling mynas are not completely covered with feathers until days 18-20, with feather elongation still occurring at fledging.

Development of Endothermy and Homeothermy

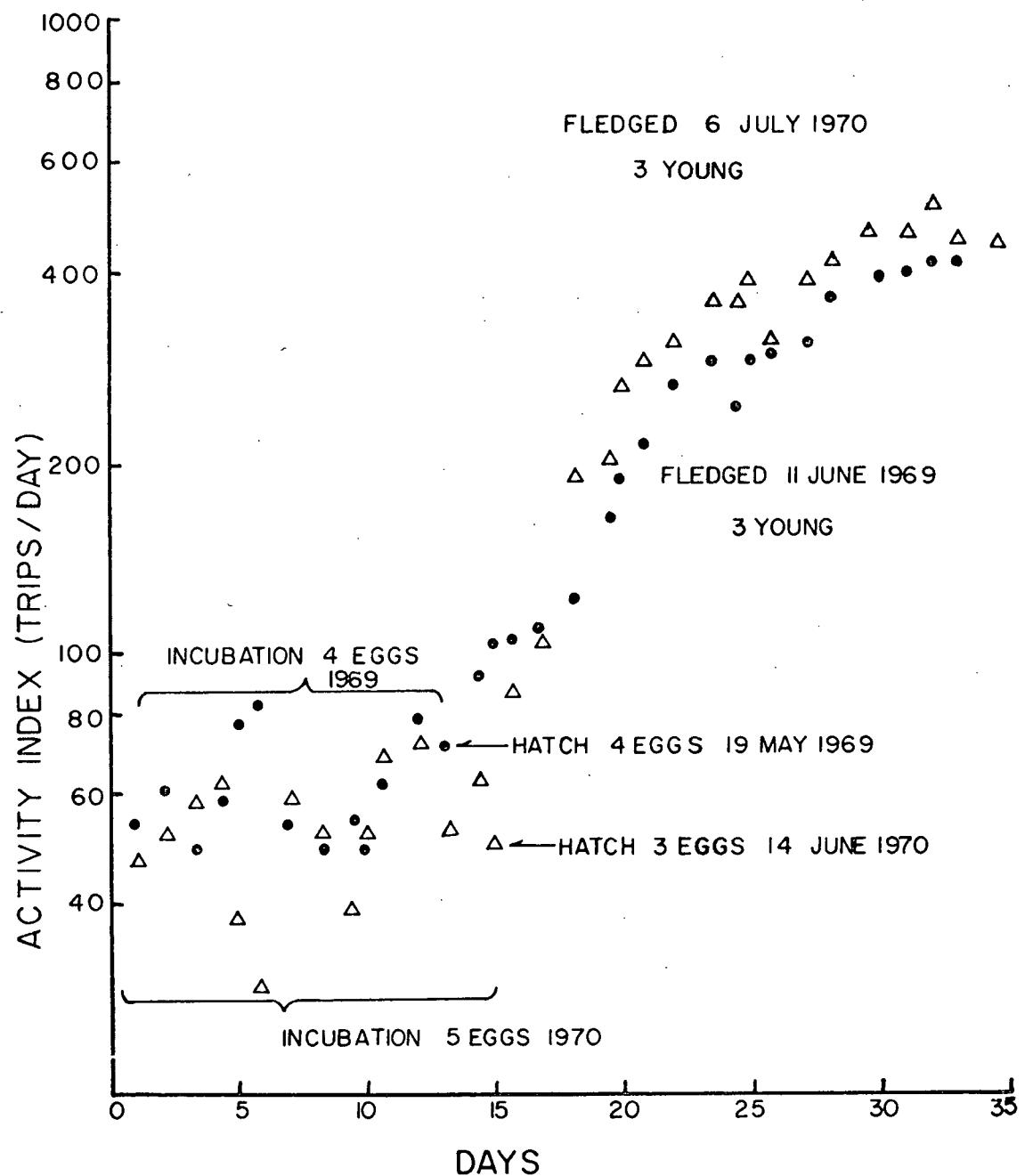
Nestling mynas are poikilothermic until day 14-16 (60-70 gm weight class) when increased metabolic activity and developing plumage enabled the bird to trap a layer of warm air for insulation. Although heat production increased (similar to starlings, Figure 8) nestlings were not completely

homeothermic until 80-85 gms. Nestling mynas also withstood extreme hypothermy during 30-minute trials at -5°C (Figure 9).

Nestling Food Intake

During the growth period, the rate of food intake of nestling mynas increased at a rate similar to starling nestlings. Figure 11 illustrates activity at two myna nestboxes (1 in 1969 and 1 in 1970) during incubation and growth. From hatching until days 12-14, a steady increase in activity was recorded. Mynas were not as industrious at feeding young as starlings. Only an 81% feeding ratio was observed (actual feedings/total trips to the nestbox). By applying this feeding ratio to Figure 11, we arrive at an initial feeding rate of 0.80 feedings/nestling-hour (18 hour feeding day), and a rate of 8.1 feedings/nestling-hour at days 14-16 (18 hour feeding day). The mean (pooled for all periods) caloric value of nestling food materials was $4.97 \pm .612$ kcal/gm (37 samples analyzed) and the mean dry weight of those food items was $0.10 \pm .048$ gms/feeding. Applying these values, in turn, to Figure 11 we obtain a description of G.E. intake for nestling mynas throughout the growth period. This G.E. increased from 0.402 kcal/nestling-hour (7.22 kcal/nestling-day) at hatching day to 4.02 kcal/nestling-hour (72.30 kcal/nestling-day) at day 14-16.

Figure 11. Adult activity at 2 myna (1 in 1969 and 1 in 1970) nestboxes.



Nest and Egg Manipulation Experiments

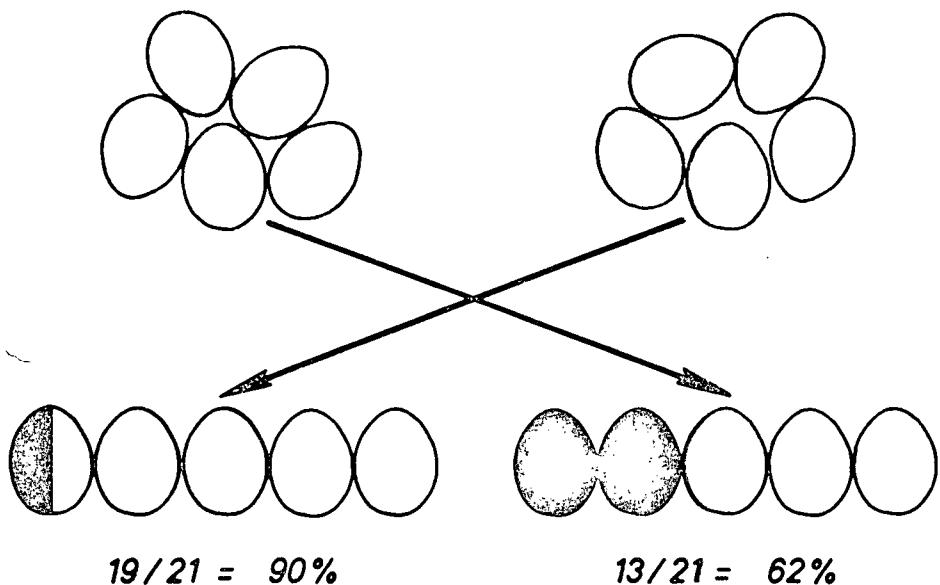
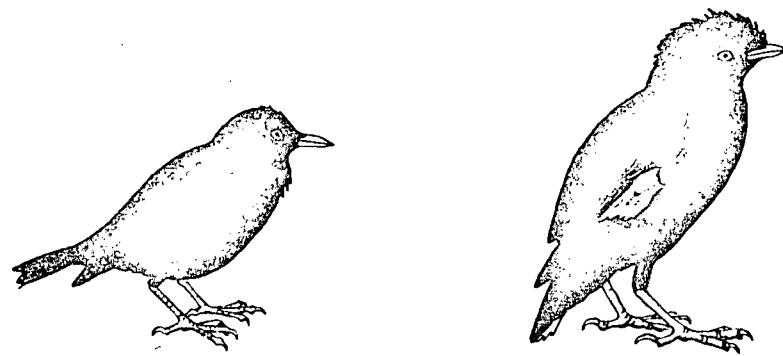
Cross-fostering Between Species

Differences between starling and myna incubation and fledging success prompted egg switching experiments between the two species to determine if these differences arose from differences in (1) egg quality or (2) the effectiveness of the adult birds as incubators and parents. Five myna and five starling clutches (5 eggs) which were synchronized (± 1 day) in their incubation cycles were switched at day 2 and followed through incubation to hatching and fledging. As Figure 12 shows, a 90% hatching success was observed for myna eggs incubated by starlings while only 62% of the starling eggs incubated by mynas hatched. Growth rates of the cross-fostered nestlings were not significantly different from those described earlier (raised by their own parents).

Heated Nestboxes

Inasmuch as one of the striking differences between the nest performance of the two species was the higher average egg temperature maintained by the starling, I investigated the influence of nest temperature upon hatching success in the myna. To do this, 5 heated nestboxes were placed in locations where mynas had already

Figure 12. Results of egg switching experiments and subsequent adult incubation by Vancouver Sturnidae.



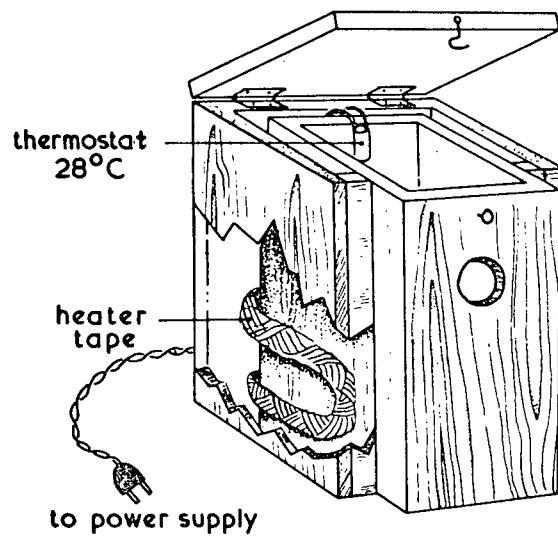
established themselves as nestbox breeders. These boxes were thermostatically regulated to keep egg level temperatures from dropping below 28°C. As shown in Figure 13 a 92% hatching success was observed in the heated nestboxes, and a 63% hatching success was observed in the controls (2 control nests were not in nestboxes, but in natural tree cavities). This success in the controls was not significantly different from the 61% success observed in 31 first clutches reported earlier.

The Energy Cycle

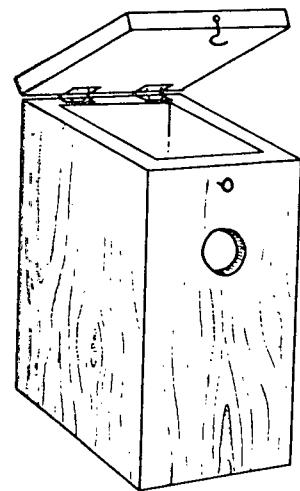
The Starling - Gross Energy

Sturnid gross energy (G.E.) intake and cage area ambient temperature fluctuations throughout the one-year experimental period are represented in Appendix Figure 1. Mean G.E. values during the excretory sampling periods are presented on a monthly basis in Figure 14. Starling G.E. intake gradually decreased from January through December with high values ranging between 118.8 and 128.32 kcal/bird-day recorded between January and April. Low intakes of 94.2, 99.1 and 97.6 kcal/bird-day were recorded during October, November and December, respectively.

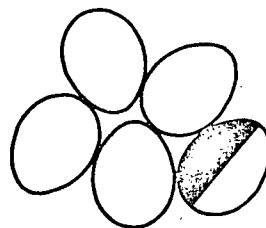
Figure 13. Results of heated nestbox experiments. Myna nestbox temperatures were prevented from dropping below 28°C; the resulting hatching success is compared with control nests.



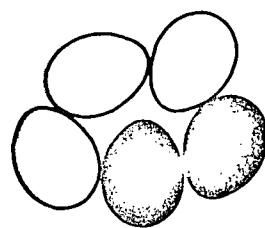
HEATER BOX



CONTROL



$$25/27 = 92\%$$



$$14/23 = 64\%$$

Excretory Energy

Starling excretory energy (E.E.) is illustrated graphically in Figure 14 also. Highest E.E. values for starlings were obtained during March and April; 73.1 and 68.9 kcal/bird-day, respectively, and the lowest value was obtained from the November sample; 40.9 kcal/bird-day. Excretory energy fluctuated more than G.E. therefore the resulting metabolizable energy (M.E.) fluctuated greatly also (Figure 14).

Metabolizable Energy

The highest starling M.E. (G.E. - E.E. = M.E.) was recorded in February (60.9 kcal/bird-day) and the lowest during October (41.88 kcal/bird-day).

Efficiency of Food Conversion

Caloric value of sturnid excretory material and digestion efficiency ($M.E./G.E. \times 100$ = digestion efficiency) both indicate the efficiency of food conversion (Figure 15). The mean monthly energy content of starling excretory material fluctuated between 4.03 kcal/gm (March sample) and 4.19 kcal/gm (October sample).

Except for high November values (58.78%), starling digestion efficiency was relatively constant throughout the year.

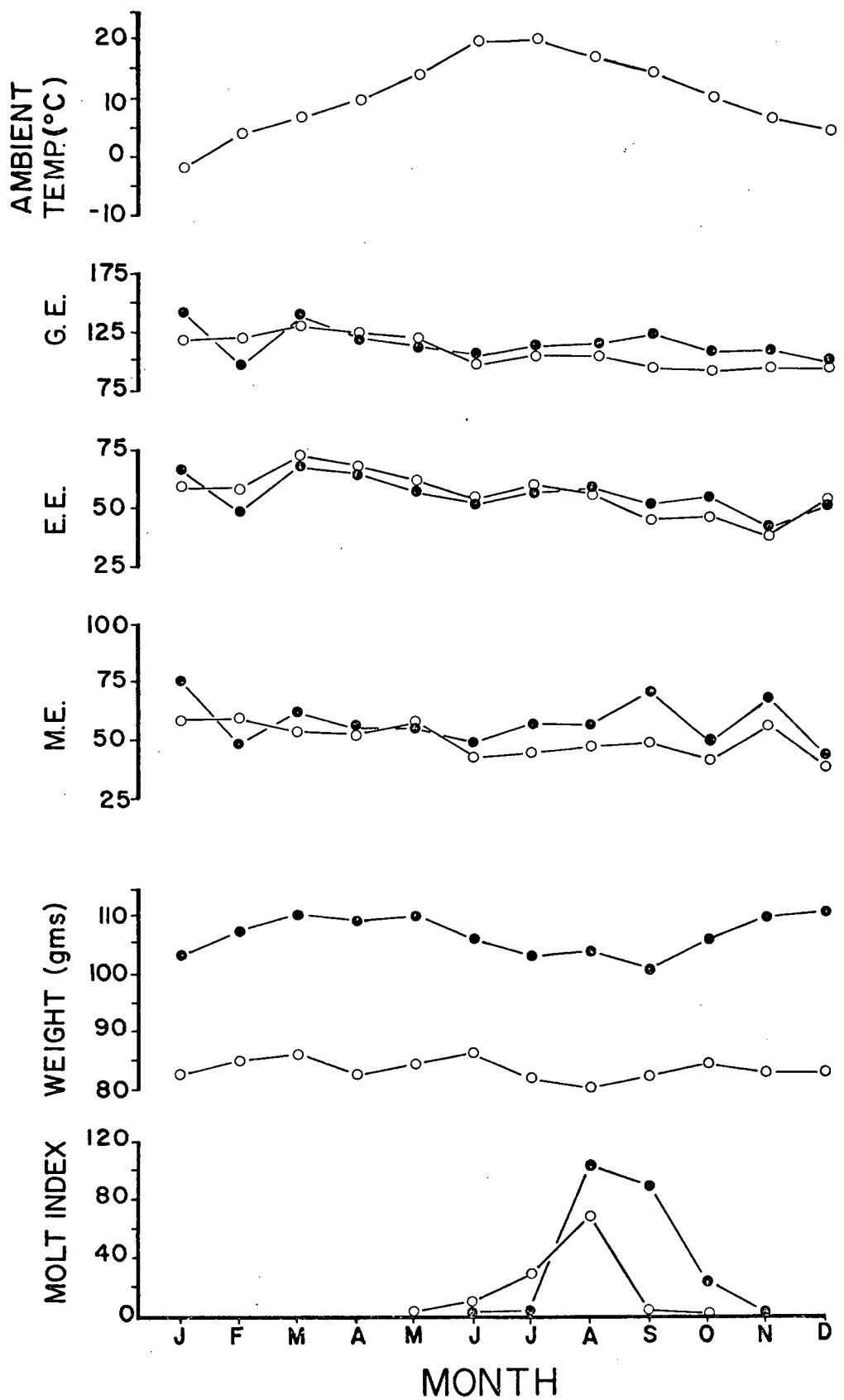
Molt

The molt is potentially a period of substantial energy drain from the bird, therefore consideration should be given this subject during exposition of results pertaining to the energy cycle. North American sturnids molt once each year during late summer and early fall. Figure 14 illustrates the pattern of molt in sturnids held captive at Vancouver, British Columbia, during the 1969 study period. Molt index is simply the number of feathers/day separated from the excreta collections. Starlings begin their molt in late June and terminate it in late August, with most feathers lost between late July and early August. Sleak iridescent contour feathers are lost first and replaced by the white-tipped winter plumage; remiges and rectrices are replaced later, with primaries 7, 8 and 9 and the outer rectrices not completely hardened until late September.

Weight Dynamics

Weight dynamics are good indicators of whether birds are maintaining energy balance. Starling weights were relatively stable throughout the year long experimental period; values ranged from 86.6 gms in late October to 80.0 gms during the molt in early August, with a yearly mean of 83.7 gms (Figure 14). Significant differences were

Figure 14. Depiction of sturnid gross energy intake (G.E.), excretory output (E.E.) and metabolizable energy (M.E.) (all in Kcal/bird-day), with molt, weight and ambient temperature changes (\circ = starling; \bullet = crested myna).



not observed for mean starling weights between or within sexes during the year.

Statistical Treatment of Energetics Data

Having described and presented the values for energy utilization by starlings, a statistical analysis of mean energy values can now be considered. Appendix Table 2 presents an analysis of variance of energy balance data. Bioenergetics data of starlings and mynas show identical trends from month to month (except for the low value for mynas in February) therefore means of both species were lumped for ease in statistical treatment. Calculated monthly constants, presented in an ordered array, when summed with the appropriate species constant (in this case, starling) and the calculated estimate of the mean, will yield a statistic which approximates the monthly parameter sought. The F values, with appropriate degrees of freedom, designate the significance of different energy values between species (myna and starling) and within months (any two months). Monthly values not connected by the same underscoring are those different from each other. In the case of starling G.E., the mean standard error of the difference between two months was 7.09 kcal/bird-day, therefore, values different by more than 7.09 (1 standard

error), were considered different. During January through May, the greatest amount of energy was consumed. Contrastingly, June and October through December were the periods of lowest energy consumption.

Starling E.E. values were treated in the same manner and are also presented in Appendix Table 2. The mean standard error of the difference between any two months was 3.51 kcal/bird-day. The calculated species constant and estimate of the mean are 0.24 and 58.64 kcal/bird-day, respectively. March E.E. was highest for starlings and the November value was lowest.

The analysis of M.E. values yields results very similar to those for G.E. (Appendix Table 2). January through May were the months when the most energy was metabolized, except for the unexplained increase in M.E. during November. Contrastingly, October and December were the months of lowest energy metabolism. The mean standard error of the difference between any two months was 5.30 kcal/bird-day and the calculated estimate of the mean was 55.64 kcal/bird-day.

The Myna - Gross Energy

Appendix Figure 1 also illustrates myna G.E. and temperature fluctuations during the one year experimental period.

Temperature and energy balance data are also compared on a monthly basis (Figure 14). Crested myna G.E. showed a decrease from January through June, after which it leveled off and remained relatively constant. The highest value recorded for myna G.E. was 143.7 kcal/bird-day during January. The lowest values were 97.96 and 102.96 kcal/bird-day during February and December, respectively.

Excretory Energy

Myna E.E. was more erratic throughout the year than G.E. High values of 66.7 and 69.7 and 64.3 kcal/bird-day were recorded for January, March and April E.E., respectively. The lowest values recorded were 43.5 and 48.0 kcal/bird-day, during February and November, respectively.

Metabolizable Energy

Myna M.E. fluctuated greatly also, especially during the second half of 1969. The high myna M.E. values of 76.9, 73.0 and 71.2 kcal/bird-day occurred during January, September and November, respectively. Low values of 49.9 and 46.9 kcal/bird-day were recorded during February and October, respectively.

Efficiency of Food Conversion

The mean monthly caloric values of myna excretory material are presented in Figure 15. The lowest and highest recorded values were 4.06 kcal/gm during May and 4.18 kcal/gm during September. Digestion efficiency of mynas ($M.E./G.E.\times 100 = \text{digestion efficiency}$) is presented in Figure 14 also. Similar to starlings, myna efficiency was highest during November (62%) and lowest during the month of October (45.94%). The trend in digestion efficiency for mynas was identical to that for starlings (Figure 15). Values for January through August were relatively stable and values for September through December were unstable.

Molt

The pattern of molt in crested mynas closely overlapped that of starlings. The molt began in mid-July with loss of the crest and facial feathers, and continued through to mid-October with the peak in feather loss during late August and early September. The last rectrices and remiges did not completely harden until early November.

Weight Dynamics

Weight dynamics of captive mynas are expressed in

Figure 15. Energy content of excreta and digestion efficiency during the 1 year experimental period (\circ = starling; \bullet = crested myna).

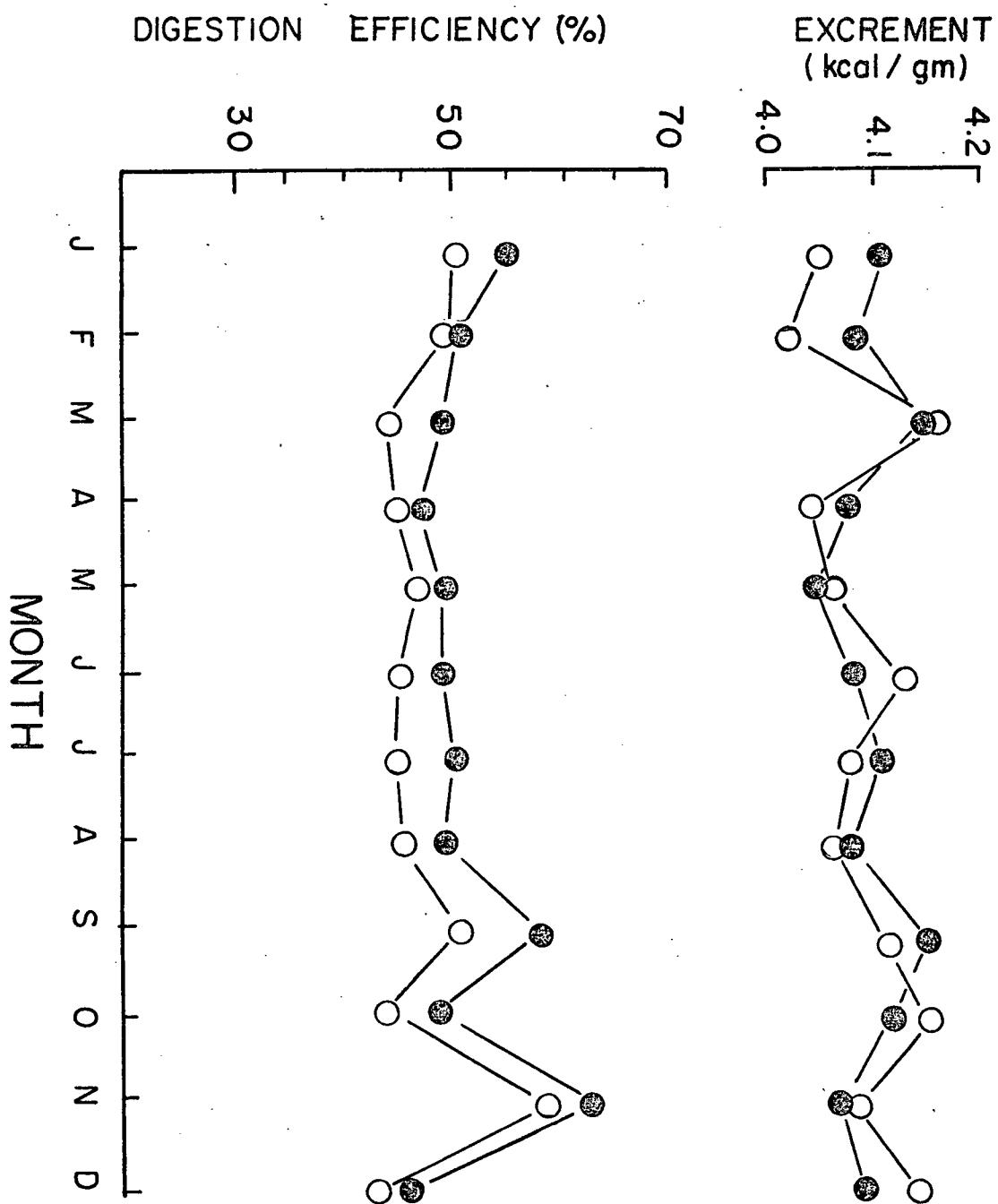


Figure 14 also. Myna weights, as those of starlings, were relatively constant throughout 1969; only the weights recorded in early May (111.4 gms) were significantly heavier than the lightest weights recorded in September during the molt (101.3 gms). It was difficult to determine sex of crested mynas without sacrificing birds, however, peaks in a bimodal distribution of weights of wild shot mynas were significantly different and were probably correlated with either sex or age. Eight female mynas weighed 107.2 ± 1.56 gms (mean \pm standard error of the mean); 9 males weighed 115.3 ± 1.28 gms. Birds were collected in winter and early spring. Determination of age by skull granulation was not attempted, therefore any influence of sex on this distribution could be masked by those of age.

Statistical Treatment of Energetics Data

The statistical treatment of myna energetics data is handled exactly as described for starlings (Appendix Table 2). Calculated monthly constants which are presented in an ordered array, when summed with the appropriate species constant and the calculated estimate of the mean, will yield the estimate of either G.E., E.E. or M.E. The values not connected by the same underscoring were considered different from others. For myna G.E., the mean standard error of the difference between any two months is still 7.09 kcal/bird-day. The calculated estimate of the mean remains 114.29

kcal/bird-day, however, the species constant has now changed to 4.37 kcal/bird-day.

For myna E.E., the calculated estimate of the mean (58.6 kcal/bird-day) and monthly constants also remain the same as described for starlings, however, the species constant has changed to -0.24 kcal/bird-day. The mean standard error of the difference between two months remains 3.51 kcal/bird-day, and as the F value for months indicates (12.45 with 11 and 372 d.f.) some months are different from others. The months considered different are those not underscored by the same line (Appendix Table 2).

Myna M.E. data are treated in the same manner as above. The calculated species constant is now 4.62 kcal/bird-day, while the remaining values (55.64 kcal/bird-day = estimate of the mean; 5.30 kcal/bird-day = mean standard error of the difference between two months) are left unchanged, except for the F values.

The periods of highest and lowest energy input, output and utilization are the same for both mynas and starlings. This simply indicates that both species responded in a similar manner to variables associated with the time of year, and is the justification used for lumping the two species for statistical treatment.

Thermal Response to the External Environment

The Starling - Effects of Ambient Temperature on Energy Utilization

Results of a regression analysis of temperature against G.E., E.E. and M.E. are presented in order to isolate the effects of ambient temperature on the energy cycle of captive sturnids. Energy values graphically presented in Figure 14 were plotted against the mean monthly cage area ambient temperature for the total, first and second half year periods (Appendix Table 3). For the first half year (January through June, 1969), only M.E. was negatively correlated (although weakly) with temperature, that is, as temperature decreased, energy utilization increased ($r=0.79$). All starling energy values for the second half year of 1969 (July through December) were positively correlated with temperature, however, only temperature versus G.E. showed a strong correlation ($r=0.80$). Year long temperature was nonsignificantly and negatively correlated with G.E., E.E. and M.E. ($r=0.29$, 0.00 and 0.45 , respectively).

The Myna - Effects of Ambient Temperature on Energy Utilization

A regression analysis of crested myna G.E., E.E. and M.E. against mean monthly cage area ambient temperature

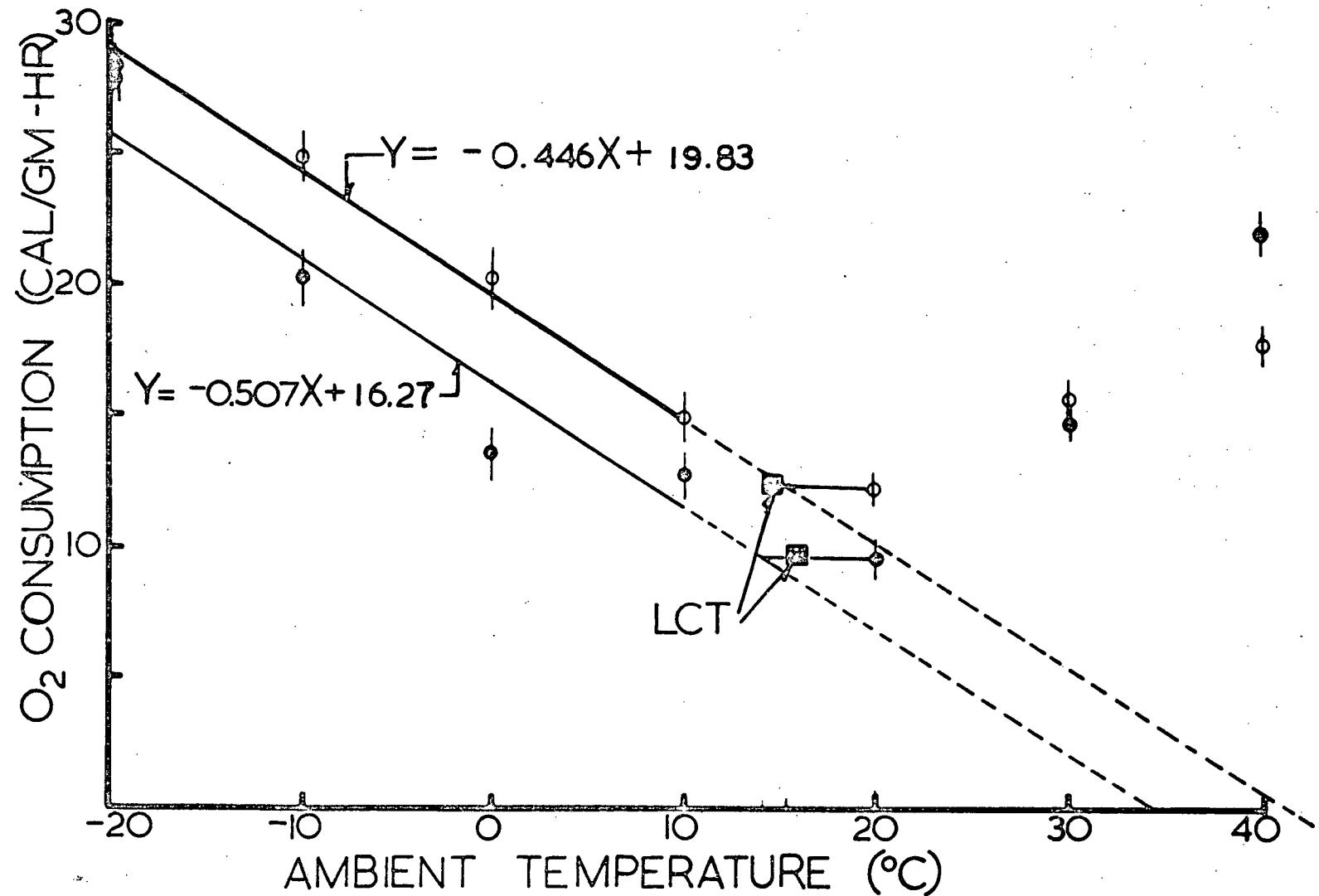
showed correlations weaker than those for starlings during the same period (Appendix Table 4). Metabolizable energy for the first half year showed the strongest negative correlation with temperature ($r=0.63$). Energy utilization data analyzed for the second half and total year periods showed weak correlations with mean monthly cage area ambient temperature.

Laboratory Studies of Thermal Response

The Starling - Oxygen Consumption

Laboratory investigations of sturnid thermal response were conducted to supplement energetics data collected in the aviary. Figure 16 illustrates the starling thermal response curve. The thermalneutral zone lies near $+20^{\circ}\text{C}$. Experimentally obtained and calculated lower critical temperatures are presented. The point where the thermalneutral zone intersects the least squares line should theoretically be the LCT. This value can be checked by using the formula: $\text{LCT} = t_b - \text{BMR}/q$, where q is the value for conductance obtained from cooling experiments (Kleiber 1965:165). For starlings, the calculated LCT of 14.70°C , using a body temperature of 40.66°C ($n=38$) and a BMR of

Figure 16. Sturnid thermal response curves illustrating theoretical LCT and experimentally observed LCT, and least squares regression lines extrapolated to observed body temperatures. Actual body temperatures at +20°C are 40.66°C and 39.93°C for starlings (n=38) and mynas (n=32), respectively (\circ = starling, \odot = myna; verticle bar through symbol = ± 1 s.e.).



12.6 cal/gm-hr, is very close to the experimentally obtained value (Figure 16; LCT).

Lethal Temperature

The LD₅₀ for upper temperature tolerance by starlings was not obtained in this study. Starlings withstood +40°C for 3 hours even though body temperatures increased an average of 2.5°C over the value obtained before birds were subjected to experimental temperatures (Table 1). No facilities were available for testing birds below -20°C, therefore no lower tolerance limits could be determined. Weight loss during metabolic trials was attributed to water loss, tissue oxidation and excretion. No attempt was made to measure respiratory water loss. Excreta lost weight during metabolic trials, therefore no values for tissue oxidation could be obtained from weight measurements.

Seasonal Effects on Metabolism

Starling metabolic trials were conducted at -20°C and +30°C in both late spring (June) and late fall (November). No significant differences in metabolic rates were found between these different seasons.

Table 1. Change in body temperature (t_b) and body weight during metabolism experiments.

<u>Experimental Temperature (°C)</u>	<u>$t_{b_0} - t_{b_1}$ (°C)</u>		<u>$w_o - w_1$ (gms/hr)</u>	
	<u>Starling</u>	<u>Myna</u>	<u>Starling</u>	<u>Myna</u>
-20	.42 ± .085 ¹	-.11 ± .182	1.18 ± .033	1.73 ± .099
-10	.48 ± .167	-.04 ± .225	.91 ± .106	1.44 ± .078
0	.53 ± .257	-.04 ± .340	.83 ± .090	1.25 ± .173
10	.80 ± .284	.51 ± .158	1.09 ± .051	1.29 ± .058
20	1.12 ± .157	1.94 ± .411	.43 ± .028	.59 ± .037
30	1.51 ± .120	1.40 ± .193	1.63 ± .119	1.69 ± .086
40	2.58 ± .187	3.57 ± .120 ² 4.70 ± .286 ³ 4.20 ± .279 ⁴	2.02 ± .076	3.77 ± .714 ¹ 2.08 ± .194 ² 3.04 ± .517 ³

¹ Mean ± standard error of the mean

² Birds that survived (n=4)

³ Birds that died (n=4)

⁴ Total birds that lived and died (n=8)

Respiratory Quotients and Shivering

Respiratory quotients (R.Q.) determined at -20°C and +20°C for starlings (0.74 ± 0.07 and 0.73 ± 0.06 , respectively) were not significantly different from each other.

Observations of starlings during metabolism experiments revealed shivering at and below 0°C. Shivering was not observed above 0°C.

The Myna - Oxygen Consumption

The crested myna thermal response curve is also shown in Figure 16. The calculated LCT of 15.34°C for mynas, using a body temperature of 39.93°C (n=32), is similar to the value obtained from the least squares line in Figure 16. This LCT, along with the BMR (9.5 cal/gm-hr) placed the myna thermalneutral zone around 20°C.

Lethal Temperature

The LD₅₀ for upper temperature tolerance in crested mynas was between 30°C and 40°C (n=8 birds); 4 died after considerable loss of weight and during hyperthermy, when tested for 3 hours at +40°C.

Seasonal Effects on Metabolism

The effect of season on myna metabolic rates was tested by measuring myna metabolism in late spring and

late fall; as with starlings, no such change was observed.

Myna R.Q. at +20°C (0.74 ± 0.08) was not significantly higher than at -20°C (0.71 ± 0.09). Shivering during metabolic trials was noticed for crested mynas at and below 0°C.

Insulation and Thermal Conductance

Cooling Experiments

Since metabolic trials suggested mynas were producing proportionally more heat than starlings at both low and high temperatures (Figure 16), an attempt was made to determine the effectiveness of plumage as an insulative layer for both species. The results of cooling experiments were plotted and regression lines relating cooling rate to external temperature were constructed for feathered and unfeathered starlings and mynas (Appendix Figures 2 and 3, respectively). Thermal conductance values were obtained using methods similar to those described by Morrison and Tietz (1957) and are expressed in $\text{cal}/\text{cm}^2\text{-hr}^{-\circ}\text{C}$. The specific heat of bird tissue was assumed to be close to 0.83 $\text{cal}/^\circ\text{C}\text{-gm}$, which is the value given by Morrison and Tietz (1957) for small mammal tissue. Table 2 presents the pertinent data from which thermal conductance values

Table 2. Conductance values obtained from cooling curves of sturnids

Weight (gms) Feathered	Weight (gms) Unfeathered	Feather Weight	Calculated Surface Area from Unfeathered Weight (cm^2)	Cooling Constants (hr^{-1})	Thermal Conductance ($\text{cal}/\text{cm}^2 \cdot \text{hr} \cdot {}^\circ\text{C}$)
<u>Starling (n=5)</u>					
88.2±.77 ¹	79.8±.95	6.3±.32	195.7±1.55	.62±.035	1.74±.114 .21±.012
<u>Myna (n=4)</u>					
112.4±5.62	100.6±1.53	10.5±.35	228.1±2.43	.50±.030	1.56±.141 .18±.012

¹: All values are expressed as means ± standard errors of means.

were calculated. All calculations for thermal conductance are based on unfeathered weights.

Surface Area

Surface area values were calculated from unfeathered weights after a series of experiments were conducted to test the accuracy of the formula given by Meeh (1897): Surface Area (cm^2) = $kW^{2/3}$. A value of 10.4 was given by Rubner (1902) for k, therefore the formula used was S.A. = $10.4(\text{unfeathered } W)^{2/3}$, where W is expressed in gms (See Figure 17).

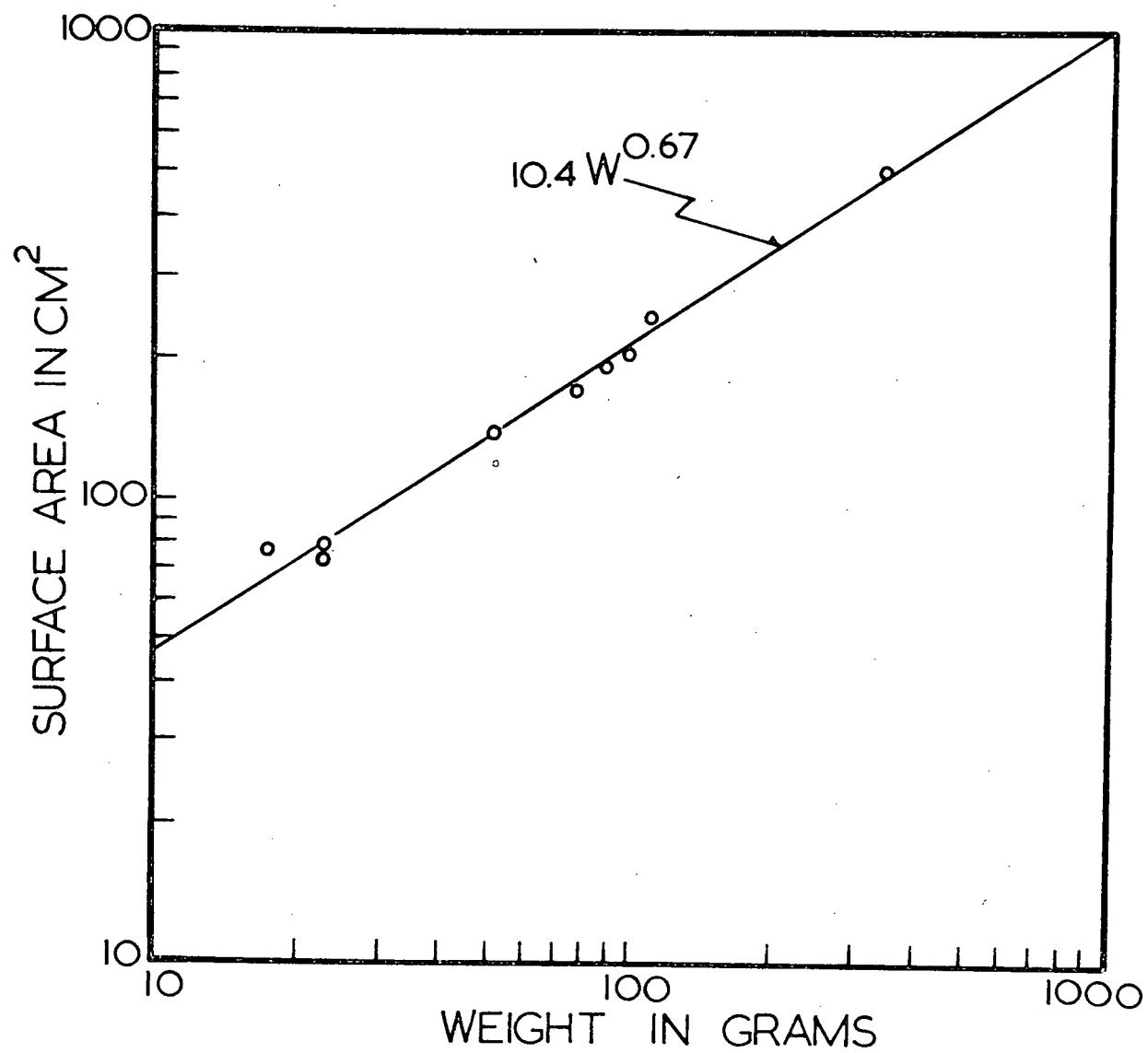
In order to evaluate plumage quality, the value L was derived as follows:

$$L = \frac{(q_2 - q_1)(\text{specific heat})(\text{unfeathered weight})}{(\text{surface area})(\text{feather weight})}$$

where q_2 and q_1 are cooling constants for unfeathered and feathered carcasses, respectively (Table 2). Thus, the value L represents the amount of heat (calories) conserved by one gram of feathers over 1 cm^2 of surface area in 1 hour for every 1°C of temperature gradient ($t_b - t_a$).

Starling L = $6.2 \pm .05 \times 10^{-2}$ cal/gm-hr- $^\circ\text{C-cm}^2$, while the mean plumage weight of starlings (n=5) collected for cooling experiments was $6.3 \pm .32$ gms (7% of total body weight).

Figure 17. Comparison of experimentally obtained (o) and theoretical (Meeh 1897: $10.4 W^{2/3}$) surface area values for 9 birds ranging in size from a juvenal barn swallow to an adult rock dove.



Myna $L = 3.4 \pm .40 \times 10^{-2}$ cal/gm-hr- $^{\circ}\text{C-cm}^2$, and mean plumage weight ($n=4$) was $10.5 \pm .35$ gms (9.4% of the total body weight).

DISCUSSION

This study has been devoted to exploring the comparative performance of two passeriformes, belonging to the family Sturnidae, as colonizers in a new environment in western North America. One of the species (Sturnus vulgaris) is of north temperate origin, the other (Sturnus cristatellus) is predominantly subtropical.

Preliminary consideration of known facts of the life history of the two species led to the proposition that the most probable differences in performance in the colonizing success of the species was concerned with utilization of the energy resources of the environment and in adaptation to thermal constraints.

To explore these areas, observations and experiments were designed to examine reproductive efficiency through the nesting period; rate of growth and course of development, with particular reference to the acquisition of endothermy; the energy cycle during the winter; metabolism under controlled thermal conditions, and the insulative quality of the plumage.

Nesting

Nesting activities by mynas and starlings started about the same time in the Vancouver area, and the dates of first eggs laid were also similar for both species, but starling activities were synchronized into definite peaks for the whole breeding season.

The onset of egg laying by mynas was very similar to that found by MacKay and Hughes (1963) for crested mynas in the Vancouver area in 1959 and 1960; first eggs were found in the second week in April. They reported a lower clutch size than that found in this study (Table 3). The largest number of myna nests had 5 eggs (47%), with 4 eggs second most common (26%), which compares favourably with results reported by MacKay and Hughes (1963:159). It is interesting to note that in the Hong Kong area, where first eggs were reported from 15 April onward, a 4 egg clutch was most common for this species (Vaughn and Jones 1913). Smaller clutch size in tropical species is common (Skutch 1949), however, it is interesting that a tropical bird appears to have increased its clutch size when moved to a temperate environment.

Wilkinson (1929:124) reported that two broods a year is typical of crested mynas in China. MacKay and Hughes reported no certain second clutches for crested mynas in

the Vancouver area, but several instances suggested that second clutches were laid. Only five certain two brood nests were found in this study, which also suggests that second nestings are not common in the Vancouver area. Scheffer and Cottam (1935) suggested the small number of second broods is the result of a lengthened period of activity associated with the first nesting. They observed a 14-day nest building period for Vancouver crested mynas, followed by a 15-day period for egg laying and incubation. The young left the nest when about 27 days old, thus the total nesting period lasted about 66 days.

Nest building took as long as two weeks for five pairs in my study, and most juveniles left the nest at 22-23 days. A total of 49-59 days lapsed from initiation of nest building to independence of the first brood.

Initiation of starling nesting activity was earlier than noticed for mynas, although not as early as reported for starlings in Arizona (Royall 1966) or Mississippi and Virginia (Kessel 1957). Starlings in the Vancouver area (49° N latitude) start first clutches earlier than suggested by the schedule of laying at $48-50^{\circ}$ N latitude for Eastern North America (Kessel 1957:270). However, peaks of egg laying by starlings in Czechoslovakia (Havlin personal communication 1968), Scotland (Anderson 1961) and Denver,

Colorado (DeHaven personal communication 1969) are close to those observed in Vancouver (15-30 April).

Clutch size for first nestings of the European starling in Vancouver (Table 3) were similar to those in New York (Kessel 1957), Holland (Lack 1948) and Scotland (Anderson 1961), but higher than reported in Arizona (Royall 1966) and Northern England (Lack 1948). Similarly, clutch size in second nestings was generally higher in Vancouver starlings than reported elsewhere, with the exception of certain locations and years in Arizona (Royall 1966) and Scotland (Anderson 1961).

Incubation

Crested mynas incubated approximately two days longer than starlings (14 and 12 days, respectively), with the mean attentiveness during daylight hours (0300-2100 hrs) for mynas 47% compared to 70% for starlings (59% and 77% respectively, for the whole 24-hour period). Myna attentiveness was significantly lower except for the 1800-2100 hour period when no significant difference was observed between the two species. Delvingt (1963) reported a 78% attentiveness (during a 24-hour period) for starlings in Belgium, which compares favourably with 77% obtained in this study.

Also, nestbox temperature at egg level was lower for incubating mynas than for starlings. However, no data were found in the literature concerning incubation temperatures for starlings.

No information was found concerning incubation for crested mynas, but Sengupta (1968) described incubation for the similar common myna (*Acridotheres tristis tristis* L.) in West Bengal as irregular (mean extreme air temperature= 20° and 32°C), with incubation left to the heat of the sun and short sitting periods during the day.

Hatching and Fledging

Crested mynas hatched far fewer eggs than starlings in this study (Table 3). A similar low hatching success was observed for the crested myna in the Vancouver area by MacKay and Hughes (1963). They found a 37% hatching success for all eggs in 1959 and 1960 with about 73% of the failures attributed to incubation failure and 20% due to egg destruction; this yields an incubation success of 49%, still lower than that found in this study. However, MacKay and Hughes observed a higher fledging rate for young mynas, from hatching, than in this study. These hatching, fledging and nesting success values are much lower than reported by Sengupta (1968) for common mynas

Table 3. Comparative reproductive data for starlings and mynas

Source	Clutch size (Mean eggs/clutch)	Hatching success (% hatched)	Nesting success (% fledged of clutch)
<u>Starling</u>			
This study	5.5 (4.8) ¹	84 (69)	76 (71)
Kessel (1957)	5.5 (4.1)	81 (71)	81 (68)
Anderson (1961)	5.2 (4.6)	88 (83)	80 (80)
Dunnet (1955)	5.1 (4.6)	88 (86)	82 (72)
Lack (1948) ²	5.2 (4.3)	85 (86)	83 (78)
Royall (1966)	4.4 ---	84 ---	57 (47)
<u>Myna</u>			
This study	4.9 (3.8)	61 (58)	46 (39)
MacKay and Hughes (1963)	4.4 ---	37 ---	31 ---
Sengupta (1968)	3.8 ---	98 ---	76 ---
Lamba (1963)	--- ---	87 ---	--- ---

¹ Values in parentheses are for second nestings (exclusive of renestings)² For Dutch starlings only

in West Bengal. He observed a hatching success of 98% for 45 eggs in 12 clutches, which is extremely high, even when compared to the 87% hatching success observed for the same species in a different part of India (Lamba 1963). The overall nesting success observed for common mynas was 75.55% (Sengupta 1968).

Nesting success for early nesting starlings in Vancouver was lower than that reported for this species by Kessel (1957) in New York, Anderson (1961) in Scotland and by Lack (1948) for Dutch starlings. Arizona birds (Royall 1966) had a lower nesting success for first clutches which was probably a result of human interference, ectoparasitic (fowl mites) infestations and overheating in the nestboxes (Royall 1966:201). Second clutches of starling eggs in Vancouver yielded a lower nesting success than the first, however, the percent fledging from eggs of second clutches is within the range of experience elsewhere (See Table 3).

Growth

The rate of starling growth ($K = 0.416$) is faster than that observed for crested mynas ($K = 0.284$) and past day 3, regression lines constructed from logistic conversion factors (Figure 7) are significantly different ($\alpha = 0.10$) from each other. The rate of starling growth in Vancouver is similar

to that reported by Ricklefs (1968:110) for Czech starlings ($K = 0.412$) and slightly faster than reported for Scottish starlings ($K = 0.396$). Also, starling growth fits nicely into Ricklefs' (1969:1032) regression line of adult body weight and growth rate (K) for temperate zone passerines. The growth rate of the tropical crested myna in Vancouver is much lower than predicted from his curve, which is consistent with the hypothesis and results presented by Ricklefs for other tropical birds.

It is interesting to note that tropical common mynas began incubation before laying the last egg (Sengupta 1968). This resulted in some nestlings hatching earlier than others, thereby increasing the rate of growth in these earlier hatched nestlings. Despite these differences in rate of growth between nestlings, development of plumage was still synchronized with age, and fledging success was high. The above-mentioned phenomenon was not observed in Vancouver crested mynas, where the growth rate of all nestlings was similar. Therefore, comparisons of growth rates of common and crested mynas using the method described by Ricklefs would not be realistic. Logistic conversion factors could be calculated for each individual nestling using different asymptotic weights measured at the nest, but these would not represent or be comparable to nestlings which reach near adult weight while still in the nest.

Few studies of comparative energetics have been made on closely related species from different geographic regions, however, Maher (1964) presents data showing that the growth rate of two arctic breeding emberizinae at Barrow, Alaska, were not different even though the adult weight of one species was 30% heavier than the other. He went on to compare growth rates of the two arctic breeding fringillids with five temperate breeding relatives and concluded that there was no evidence for adaptation in growth rates in widely dispersed members of the same family. Crested mynas and European starlings, although similarly related, have evolved in two different climatic and ecologic (tropical and temperate) regions. I have shown the rates of growth to be different as also demonstrated by Ricklefs (1969a); this reinforces the suggestion that differences between tropical and temperate regions are much greater than those between arctic and temperate regions, with respect to the evolution of breeding systems, mortality, and the growth of passeriform birds.

Nestling Energy Intake

Values for sturnid feeding rates are given by Havlin and Folk (1964), Kluijver (1933) and Dunnet (1955) for starlings and by Sengupta (1968) for mynas in West Bengal.

Dunnet listed only wet weights of food, which consisted mostly of cranefly larvae (80%) and earthworms (16%). Assuming a maximum of 80% water content for these food items, we can estimate an average of 0.366 gms/feeding from Dunnet's Table 3 for a nest of three 18 day old nestlings, which is about three times the value obtained from calculations in this study. Dunnet mentioned that his data did not substantiate Kluijver's observation that the average size of the feed increased gradually until the nestlings were 12-15 days old. However, he did mention that the daily amount of food necessary for a nestling to follow the mean growth curve rises quickly to a maximum at about day 10, and this is maintained until a few days before the nestlings leave the nest at about 22 days old.

Recordings of adult feeding activity in my study (Figure 10) substantiate Dunnet's last statement and also show the same trend for myna feeding activity. Although the size of the food items theoretically could increase as the nestling's appetite and mouth size increase, my data suggests that most of the increase in nestling food intake was the result of an increased feeding rate rather than an increase in the size of the food items supplied.

Kluijver (1933) found that the wet weight of foods/feeding never exceeded 1 gm. The maximum dry weights of feedings reported by him could not have been larger than 0.20 gms/feeding if we still assume an 80% water content for food brought by Dutch starlings (primarily cranefly larvae); thus his values were probably lower than those reported by Dunnet. Weights of feedings in my study approximate those reported by Kluijver, however, the difference in location of study areas, and the number of assumptions involved make direct comparisons risky. Also, as mentioned earlier, values presented in this study are averages for the whole growth period.

Havlin and Folk (1964) observed late broods of starlings in Czechoslovakia and estimated 750 gms of cherries (Prunus cerasus) consumed by 5 full-grown, but nestling, starlings in one day. This value yields 24.3 gms/nestling-day of pitless dried cherries consumed, which in turn yields approximately 120 kcal/nestling-day of G.E. intake for late broods of starlings in Czechoslovakia. This estimate is higher than the 83.50 kcal/nestling-day obtained for first broods of starlings in this study. The discrepancy may arise, in part from the values used by me in converting Havlin and Folk's (1964) gross weights into energetic terms. I used values obtained from cultivated Byng cherries in the

Vancouver area where water content was 78%; pits represented 5.7% of the total cherry weight, and energy content was 5.01 kcal/gm.

Westerterp (1971) has made extensive studies of energy balance during growth of nestling starlings in Holland. Compared with results from his more detailed analysis, my estimates of energy intake by nestlings in the Vancouver area are about 20% higher in the earlier stages of growth and about 40% higher at later stages of growth. The estimates I obtained by calculation from the data of Havlin and Folk (1964) are over 100% higher than Westerterp's estimates for Dutch starlings at comparable weights.

Although the rate of nestling growth, as recorded by Westerterp, is almost identical to that recorded in this study, the asymptotic weights of Vancouver nestlings are almost 10 gms heavier than the Dutch birds. Also, mortality was high among the Dutch starlings; after subtracting known mortality as a result of investigator interference, still only 30% to 49% of all eggs laid resulted in fledged young. However, the most significant factor affecting the discrepancy in energy intake values between the two studies is probably the difference in nestling energy metabolism by Vancouver starlings compared with those invest-

igated by Westerterp. Even after correcting for the fact that Westerterp's birds were grouped during metabolism trials (See Breitenback and Baskett, 196), Vancouver nestlings in the 60-70 gms weight class produced heat at a rate over 1.5 times (See Figure 9. 35 kcal/nestling-day compared with 18 kcal/nestling-day) that of the Dutch birds in the same weight range. Both Dutch and Vancouver birds weighing less than 40 gms had a similar energy expenditure (10 to 15 kcal/nestling-day).

Sengupta (1968) found that feeding rates in the tropical common myna in West Bengal increased steadily with growth and development. He reported 1.96 feedings/nestling-hour at day 1 and 4.26 feedings/nestling-hour at day 16, thus his values for common mynas were higher than mine for crested mynas during the early stages of growth and lower in later stages.

Starling food habits in Europe and North America have been described by Dunnet (1955), Anderson (1961), Havlin and Folk (1964), Szijj (1957), Kalmbach and Gabrielson (1921), Besser, DeGrazio and Guarino (1968) and others. However, only a few food habits studies have been made of crested mynas (Scheffer and Cottam 1935; Wood 1924). No studies have been made of comparative food habits of sympatric mynas and starlings, however, the data of Scheffer

and Cottam are best suited for such a comparison. They found that mynas consumed more vegetable (61.11%) than animal matter (38.89%); starlings collected during the same period but at different locations consumed more animal (62.29%) than vegetable matter (37.71%).

Species differences in food selection have been demonstrated in the present study where mynas and starlings fed over the same region. In general mynas included a higher percentage of low energy and low protein content vegetable foods in the nestling diet. Early in the nesting season, both adult starlings and mynas included animal matter as the major portion of food delivered to young. Analysis of these food items delivered prior to 1 July revealed that nestling starlings were fed 69% animal matter, 19% vegetable matter, with the remaining 2% composed of undigestible synthetics and mineral. Mynas fed their nestlings 66% animal and 24% vegetable matter during the same period.

After 1 July, starlings fed their young 61.5% animal matter and 38.5% vegetable matter. However, vegetable and animal material represented 67.2% and 22.8% respectively, of the myna diet during the same period.

Both adult and larvae Hymenoptera and Lepidoptera, larvae Tipulidae and adult oligochaets were the major animal food fed nestlings throughout the breeding season by both species. Fruits, mostly cultivated and wild

Prunus spp., Rubus spp., cultivated Malus spp., and Vaccinium oxycoccus were the primary components of the vegetable diets of both myna and starling nestlings, with heaviest use of these species occurring later in the nesting season.

Development and Plumage of Endothermy

The development of starling plumage follows the description given by Kessel (1957) for starlings in New York. The rate of growth of the longest primary was used as a general index of plumage development. That rate is similar in both starlings and crested mynas, however, first appearance of primaries is on day 5 for starlings and days 6-7 for mynas. Primaries began to develop in common mynas (Sengupta 1968) on day 7-8, which is later than that observed for crested mynas in Vancouver (Figure 6). The rate of growth of primaries in the common myna in West Bengal is greater than that of birds I studied. Thus, at 10 days post hatching the common myna had a primary length of 4 cm compared to 2 cm for Vancouver crested mynas on the same day. This difference may reflect species differences or factors associated with the environment.

Contour feather development is very similar in common and crested mynas with both species almost fully fledged by days 22-24, after which both species are fed and protected by both parents. This period lasted for nearly one

and a half months for both the common myna (Sengupta 1969) in West Bengal and the crested myna in Vancouver.

Endothermic contribution to the overall heat balance of nestling altricial birds is small, with most heat provided by brooding parents (Baldwin and Kendeigh 1932). Figure 8 demonstrates the gradual increase in this endothermic contribution during growth of both species of nestlings. Complete homeothermy by Vancouver sturnids was not achieved until asymptotic weight was nearly attained. Oxygen consumption of nestlings in different weight classes has shown the pattern of development of homeothermy throughout the growth period. An increased oxygen consumption represents an attempt by the nestling to increase heat production, while the development of plumage enables this heat to be captured for insulation and subsequent maintenance of a constant body temperature. As can be seen from Figures 8 and 9, an increase in endothermy did not occur or even become partially effective until after days 10-12 for starling nestlings and days 12-14 for crested myna nestlings. There is considerable diversity in the rate at which endothermy is achieved by nestlings of altricial birds. Dawson and Evans (1957) found the development of endothermy in several species of passerines followed a pattern similar to that here described. Brietenbach and

Baskett (1967) showed a similar development of endothermy for the mourning dove (Zenaidura macroura), and Maher (1964) found arctic breeding fringillid nestlings to be essentially ectothermic from 0-4 days of age. Brenner, however, (1964) reported endothermy in red-winged blackbirds (Agelaius phoeniceus) at 1-3 days of age.

Nestling myna metabolism was lower than that of starlings at most temperatures (3-7 nestlings tested at each t_a), but only statistically different ($\alpha = 0.10$) in the 40-50 gms weight class. Myna body growth and plumage development was slower than that observed for starlings, and mynas left the nest at an earlier stage of development than starlings, therefore, differences in nestling metabolic rates are not surprising. Further, if nestling metabolic rates for starlings and mynas in the 40-50 gms weight class are compared on the basis of percent total plumage development, no difference is detected. Similarly, it is evident that the development of endothermy is not different for developing starlings and mynas (See Figure 8).

Nest and Egg Manipulation Experiments

Egg switching experiments emphasized the effects of low nest attentiveness and consequent low mean egg level temperature exhibited by mynas (See Figure 11). These

experiments offer answers to a variety of questions involving egg laying species in which aspects of parental behaviour are critical in the survival of both the young and the species. Thus, incubation behaviour was suspected to be the weak point in the myna breeding cycle. In a tropical environment where temperatures during the nesting season are higher than in Vancouver (Figure 3), a strict incubation schedule would not be critical. This is supported by Sengupta (1968) who reported a 97.77% hatching success by the common myna in West Bengal, even though nest attentiveness was low.

Egg switching experiments indicated that the differential hatching success was due to an aspect of incubation behaviour. When heaters were installed to maintain egg level temperature above 28°C, hatching success was the same for both species. The results from these experiments substantiate the findings of nest temperature recordings which indicated that egg level temperature might be the critical aspect affecting low hatching success in Vancouver mynas.

Incubation rhythm was not monitored mechanically, but checks were made on heated nestboxes periodically; no evidence was found that mynas were more nest attentive in heated than in unheated nestboxes. Von Hartmann (1956)

suggested that such changes in incubation behaviour appear when nest temperature is changed. He showed that when nest temperatures were raised experimentally, incubating adult pied flycatchers (Ficedula hypoleuca) shortened sitting periods. However, an adaptation of this sort or the inverse of it has not been demonstrated in tropical hole nesters.

Growth rates of nestlings hatched by foster parents were measured and found to be the same as for nestlings reared by their own parents. Even though egg colours differed between the two species, nest cavities were dark, egg sizes were similar and both species readily accepted each others eggs. Vocalizations of the nestling mynas are similar to those of starlings at hatching; later myna food calls became harsh and much louder than those of nestling starlings. Because of this, it was initially expected that foster parents would abandon the nestlings, however, this only occurred in one instance when a pair of starlings abandoned half-grown mynas before fledging.

All cross-fostered nestlings were colour marked to make observations of post fledging behaviour easier. However, no cross-fostered nestlings were seen after fledging.

It is interesting to speculate on the consequences of innate versus learned behaviour in cross-fostered nestlings. Experiments of this kind could increase knowledge concerning the origin of certain avian behavioural traits; especially important and revealing would be cross-fostering experiments designed to test the origin of reproductive isolating mechanisms.

The Energy Cycle in the Aviary

Gross energy intake decreased gradually throughout the entire 1 year experimental period. Both starling and myna excretory energy was more erratic than G.E. for the second half year of 1969, thereby yielding erratic values for metabolizable energy (M.E.). Crested mynas ingested significantly more energy than starlings during the year long experimental period. Also, myna M.E. was significantly higher than that for starlings for the same period. However, no significant difference existed in excretory energy output between the two species, as evidenced by the F value for species in Appendix Table 2.

Since temperatures were cold in the early half of 1969, regression analyses were conducted for the one-half year periods as well as for the total year period to isolate the effect of temperature on the energy cycle of these two

sturnids. Only the mean monthly starling M.E. for the first half of 1969 was significantly correlated (negatively) with mean monthly cage area ambient temperature ($\alpha = 0.10$). Similarly, only myna M.E. for the first half year was significantly correlated with ambient temperature. All myna energy against temperature correlations were weaker than those for starlings.

Second half year energy values for both mynas and starlings were weakly and positively correlated with cage area ambient temperature. Only G.E. showed a strong statistical correlation with ambient temperature.

No significant correlation existed between starling G.E., E.E. and M.E. values and year long mean cage area ambient temperature.

There is in most cases a stronger correlation between temperature and M.E. utilization for the first half of 1969 than for either the total or the last half of 1969. This suggests that in a normal year, warmer winter ambient temperature would play a minor role in regulating energy expenditure of these birds. Even though the winter of 1968-69 was one of the coldest recorded for the Vancouver area, no dramatic temperature-induced fluctuations in energy metabolism occurred. Also, data presented in Appendix Table 1 suggests that starlings and mynas were

similarly influenced by ambient temperature. The variability in E.E. resulted in a similar variability in M.E. for both species, except for the first 6 months of 1969 when temperature gradients ($t_b - t_a$) were extreme enough to weakly influence energy metabolism.

Starlings had no apparent advantage over mynas; G.E. and E.E. were about equally (weakly) correlated with temperature. The fact that the total year M.E. was negatively correlated with temperature indicates that a general trend (although statistically insignificant) of increased energy metabolism during colder weather was evident. Also, both G.E. and E.E. were negatively correlated with temperature, which indicates that at least in part, the birds compensated for cold by increasing the volume of energy processed rather than increasing the efficiency of utilization. No significant correlation was detected between either temperature and caloric value of excreta or temperature and digestive efficiency. This agrees with the findings of Kendeigh (1949), Davis (1955), West (1960) and Zimmerman (1965). However, it disagrees with results presented by Owen (1970) for blue-winged teal (Anas discors), Williams (1965) for Canada geese (Branta canadensis) and Brooks (1968) for redpolls (Acanthis spp.).

No significant correlation could be found between molt index or energy content of the excreta and digestive efficiency. However, a higher M.E. was observed during the molt and a subsequent lower value observed after termination of the molt, suggesting that the experimental birds did increase their M.E. during this period. This is surprising since their diet contained 20% protein, which is more than sufficient to accommodate molt in captive birds (Martin 1968). Also it is surprising that, in fact, the lowest weights recorded were during the molt period. The low mean starling weight of 80.0 gms during early August (although not significantly lower than any other period) falls during the peak of feather replacement (Figure 13). The high mean starling weight of 96.6 gms occurred in late October, after completion of the molt.

Crested mynas similarly reached their lightest weights in mid-September (mean=101.3 gms; n=18) during the peak of feather replacement. The highest mean weight (significantly higher than the low weight recorded in September) was recorded for early May (111.4 gms), however, after the molt in late fall, myna weights also increased (See Figure 13).

During June, when the mean cage area ambient temperature was 20°C, starling and myna metabolism in the

aviary was about equal: 21.95 cal/gm-hr and 20.99 cal/gm-hr, respectively. At the same temperature in the environmental cabinet, postabsorptive and resting starlings and mynas metabolized 12.6 and 9.5 cal/gm-hr, respectively, at night. Assuming the latter values are minimum rates at these temperatures, a remainder of 9.13 and 11.27 cal/gm-hr exists for starlings and mynas, respectively, to carry out activities in their cages.

In April, the mean cage area ambient temperature was 10°C and starlings and mynas metabolized 28.44 and 22.13 cal/gm-hr in their cages. During respirometric trials at 10°C, starlings metabolized 15.02 cal/gm-hr compared to a value of 12.97 cal/gm-hr for crested mynas, leaving 13.42 and 10.64 cal/gm-hr of energy available for daily activities for the respective species.

During January, the mean cage area ambient temperature of -2°C was close enough to 0°C to make further similar comparisons possible. The values at -2°C for energy metabolized outside were very similar for both species with starlings metabolizing 31.26 cal/gm-hr and mynas metabolizing 31.12 cal/gm-hr. During respirometric trials starlings metabolized 20.26 cal/gm-hr compared to 13.59 cal/gm-hr for crested mynas, leaving a remainder of 11.00 and 17.53 cal/gm-hr, respectively, for activity in the cages.

Thus, the remainder (activity energy) is about equal for starlings and mynas at 20 and 10°C, however at -2°C, requirements for mynas are about 50% greater than those for starlings. These calculations would indicate that crested mynas are either more active than starlings in the cages during cold temperatures or they have trouble maintaining energy balance at the colder temperatures. Although recorders were not used to monitor activity, birds were watched almost daily and I felt that mynas were not more active than starlings in the cage area during this study.

Starlings were more restless than mynas and spent more time preening and fluttering in early morning hours. When wild mynas came into or rested near the cage area, and especially when they vocalized, caged mynas became excited and fluttered from perch to perch. Also, on several occasions, norway rats (Rattus norvegicus) harassed caged birds and on one occasion rats killed and ate 2 starlings through the cage wires. The late February E.E. collection coincided with this period of rat harassment, and a reduced amount of excreta was observed as a result. Also, during April an adult female Cooper's Hawk (Accipiter cooperii) made visits to the cage area for several days (See Appendix Figure 1; April G.E.) before she was captured

and released elsewhere. Under such conditions of stress, birds became very excited and ate little food. However, both species were subjected to the same conditions and it is felt that mynas did not show a greater reaction during these periods of stress. Kendeigh (1970) presents a formula describing existence energy (M.E. when weight balance is maintained) requirements for 15 passerine species at 30°C ($M = 1.5720 W^{0.621}$; where M = existence energy, and W = weight in gms), for 9 non-passerine species at 30°C ($M = 0.5404 W^{0.7545}$), and for both groups at 0°C ($M = 4.3372 W^{0.5300}$). Although sturnids are passerine birds, no mean monthly value near 30°C was recorded in this study, therefore comparisons were made between my data for sturnids collected outside at -2°C (January, 1969) and Kendeigh's predicted values calculated from $M = 4.3372 W^{0.5300}$ for all species at 0°C. The predicted values for starlings and mynas respectively are 45.09 and 50.60 kcal/bird-day. Kendeigh includes standard metabolism, specific dynamic action and locomotor activity within the cages as part of his existence energy. Kendeigh stated that cages used for housing birds "varied in size to permit approximately the same amount of free movement; e.g. hopping but not flight (Martin 1967)". Cages used in my study were large enough to permit flight for several

feet and birds did so readily. The discrepancy between values obtained in my study (59.4 and 76.0 kcal/bird-day, respectively, for starlings and mynas) and those predicted by Kendeigh's equation could be attributed to increased activity by my birds.

More experiments need to be undertaken with feeding conducted at constant temperatures in controlled environment cabinets. Although the values presented give indications of general trends, many variables could be eliminated or measured by conducting more closely controlled experiments.

Metabolism Under Laboratory Conditions

Metabolic curves (Figure 6) indicate that crested myna metabolism was lower than that of starlings except at the extreme ends of the experimental temperature spectrum. Mynas had difficulty keeping warm at -20°C and keeping cool at +40°C. The upper temperature tolerance level (LD_{50}) for a three hour period was 40°C for crested mynas ($n=8$ birds), which is lower than reported (46-47°C) by Kendeigh (1969) for several other species of passerine birds. Myna lethal temperature was also lower than reported for blue-winged teal by Owen (1970), but similar to that of Canada geese (41°C) reported by Williams.

Starlings survived temperatures slightly above 40°C

for three hours showing no noticeable adverse effects, however, above 30°C both species panted vigorously. Relative humidity in the respiration chamber was close to 20% during all tests. Both species exhibited visible shivering at temperatures colder than 0°C, but mynas elevated metabolic rates at colder temperatures faster than starlings.

West (1962) suggested that most heat production in birds is a result of muscular activity. His experiments with evening grosbeaks (Hesperiphona vespertina) have shown that in both summer and winter these birds shiver all night out-of-doors at all temperatures below thermal-neutrality, and the intensity of shivering increases as the ambient temperature falls (West 1962:299). Although starlings shivered at and below 0°C, they maintained and even overcompensated to give a net increase in body temperature (Table 3), which contrasted with the net temperature decrease exhibited by crested mynas below 0°C (Table 1). Hart (1962) conducted metabolic tests (1 hour trials) on starlings at temperatures near -70°C which did not prove fatal. However, his cold resistance tests are not comparable to mine because he used time as the variable (at -48°C) rather than temperature.

Only two other sources of metabolic data are available for sturnids. Hart (1962) made estimates of starling metabolism between -65 and +38°C. All his measurements were made during daylight hours (in a darkened chamber). His values at 38°C and 30°C (1962:22) compare favourably with those in this study at 40°C and 30°C, but values at 12, 0 and -15°C are higher than those obtained in this study at similar temperatures. It should be pointed out that Hart's oxygen consumption values for evening grosbeaks are also markedly higher than those found by Dawson and Tordoff (1959). Brenner (1965) also measured metabolic rates of single roosting starlings at 2-4°C and 24-30°C. His values again are very close to mine at his 24-30°C range, but different at the 2-4°C range.

Aschoff and Pohl (1970) have compared metabolic data obtained in darkened chambers during day (Activity period) and night (Resting period) and found a mean difference of 23% with day values higher. Thus, even though respiration chambers are darkened, birds have a built-in rhythm which is not interrupted merely by turning out the lights. Lewies and Dyer (1969) illustrate this phenomenon most clearly (pp. 293-294). It is also interesting to note that at warmer temperatures the differences between day and night metabolism are less than at colder temperatures.

For example (Lewies and Dyer 1969), the mean minimum day and night metabolism values for male red-winged blackbirds (Agelaius phoeniceus) were $3.61 \text{ cc O}_2/\text{gm-hr}$ at 42.5°C and $3.04 \text{ cc O}_2/\text{gm-hr}$ between 43 and 45°C , respectively, with day 16% higher than night. The mean maximum values for day and night were 7.98 and $5.38 \text{ cc O}_2/\text{gm-hr}$ at 5 and 0°C , respectively, with day and night values different by 23%. For female red-winged blackbirds the difference was even more extreme. The mean minimum day and night metabolic values were 3.05 and $2.47 \text{ cc O}_2/\text{gm-hr}$ at 45 and 42°C , respectively, which is a difference of 19%. The mean maximum day and night metabolism values for female red-wings were 9.52 and $3.23 \text{ cc O}_2/\text{gm-hr}$ at 0° and 2°C , respectively, which is a difference of 65%.

Thus it seems the warmer the ambient temperature during experimentation, the smaller the difference in values of metabolic rate between day and night. This in part, could explain the difference between my values and those of Hart. However, it remains evident that metabolic data obtained from this study are higher than presented by Hart (See Table 4), whose corrected basal metabolism value should be approximatrly 17% lower than presented (based on the 16.6% differences presented by Lewies and Dyer 1969). The data of Brenner (1965) show much the same discrepancy from my data as that of Hart. Brenner (personal communication) performed metabolism trials in late afternoon and early evening, possibly making his values high also.

In view of these differences presented by Aschoff and Pohl, and illustrated by Lewies and Dyer, comparisons drawn between uncorrected day and night metabolic data are inappropriate. It is imperative that researchers give detailed information about time of day and techniques used during metabolism experiments.

Starling and myna standard metabolism compares favourably with the formula: $M = 0.867 W^{0.724}$; where M is resting metabolism in Kcal/bird-day for passerine birds and W is weight in gms (Kendeigh 1970). Weights of 82.9 and 107.7 gms respectively, for starlings and mynas prior to 20°C metabolism trials were used to obtain these calculated values (See Table 4).

Basal metabolic rates calculated from the following equation:

$$\text{BMR (cal/gm-hr)} = \frac{(\text{Specific heat}) (\text{Weight}) (q_1) (t_b - \text{LCT}) (\text{hrs/day})}{(\text{Weight}) (\text{hrs/day})}$$

yields values of 12.8 and 10.4 cal/gm-hr respectively, for starlings and mynas. These values are close to 12.6 and 9.5 cal/gm-hr obtained in my respiration trials. The above equation, when rearranged could also be used to estimate the cooling constant (q_1) for a feathered bird carcass.

Calculated (Kleiber 1961) lower critical temperatures (LCT) of 14.07 and 15.34°C agree with values estimated from

Table 4. Comparisons of sturnid resting metabolic rates.

Source	Resting Metabolic Rate ^a (cal/gm-hr)	
	<u>Sturnus vulgaris</u>	<u>Sturnus cristatellus</u>
This study	12.6 @ 20°C	9.5 @ 20°C
Hart (1962)	12 ^b @ 20°C	---
Brenner (1965)	10.5 ^b @ 20-24°C	---
Kendeigh (1970)	10.7 ^c	9.8 ^c

^a Metabolic rate in the thermalneutral zone during the rest period.

^b Corrected values to eliminate effects of activity-resting cycle (Aschoff and Pohl 1970).

^c Calculated standard metabolism from body weights.

Figure 16. Extrapolation of metabolism slopes through LCTs was attempted to obtain estimates of body temperatures for starlings and mynas. This technique was fairly accurate for starlings, but less satisfactory for the mynas (Figure 16). Mynas did not increase their metabolism as rapidly when temperatures became colder, which might reflect the slight differences in metabolic slope below the LCT. Since metabolic requirements are greater for aviary mynas than aviary starlings, this would seem inconsistent, however, standard metabolism at night is not a measure of existence metabolism during the day. Also, myna body temperature decreased below normal at cold temperatures during metabolism trials (See Table 1). Myna metabolism increased sharply at the -20°C level suggesting that these birds probably could not withstand long term drops in body temperature. This is substantiated by the fact that two mynas were found frozen to death in their cages in late December, 1968, when ambient temperatures were near -20°C. Also, mynas commonly huddle near chimney heat effluent with house sparrows (Passer domesticus) on cold winter days. These factors would suggest that mynas are not well adapted for a cold climate and that they have not evolved any special physiological adaptations for cold.

Plumage Quality and Thermal Conductance

The quality of plumage as an insulator was investigated for both species. Conductance values and cooling constants are presented in Table 2. Lawieski et al (1967) stated "because thermal conductance includes evaporation, conduction, convection and radiation heat loss, and these avenues are far from uniform over the surface of animal bodies, we feel that attempts to express thermal conductance on the basis of surface area (generally calculated from body weight) in small homeotherms are often unrealistic". However, if one is expressly trying to measure the value of plumage as an insulator, and recognizing that plumage plays a large part in regulating heat losses by conduction, convection and radiation, surface area would seem the appropriate unit. Weight is similarly a variable unit, depending upon the degree of fatness of the specimen or whether the crop or gut is full. Meeh's formula was found to be accurate for estimating surface area from bird weights (Figure 17), and values obtained by this formula were used in my calculations.

Thermal conductance equations have been published by Herrried and Kessel (1967) and Lasiewski et al (1967) for various passerine and non-passerine birds. My values

are not significantly different from predicted values. Herried and Kessel calculated thermal conductance similar to the method described by Morrison and Tietz (1957), whereas Lasiewski et al calculated thermal conductance indirectly from metabolic rates. Theoretically, these two techniques should produce similar results.

The exact surface from which body heat is released can be argued, however the skin should be the standard surface accepted. This would eliminate the effects of gradients between the skin and feathers which vary with the posture and basic structure of the feathers. The advantages of using live birds are obvious and give some support to the technique of Lasiewski et al (1967), and Wallgren (1954), however, if the feathers are to be removed in an effort to evaluate plumage quality, live birds cannot be used. Therefore it is useful to explore the technique using fresh bird carcasses. If the skin surface is to be accepted as the standard surface, the unfeathered weight should be employed in all calculations. Feathers do not contribute significantly in specific heat determinations of bird tissue, therefore, their inclusion in such calculations is questionable.

The mean value ($n=4$) for myna plumage quality is $3.4 \pm .40 \times 10^{-2}$ cal/gm-hr- $^{\circ}\text{C-cm}^2$ compared to $6.2 \pm .50$

$\times 10^{-2}$ cal/gm-hr- $^{\circ}$ C-cm 2 (n=5) for starling plumage. These values suggest real differences in basic plumage quality of starlings and crested mynas. It is interesting to note that both mynas and starlings have more feathers, by weight, than predicted by Kendeigh's (1970) equation:

$W_f = 0.068 W^{0.95}$; where W_f is weight of the feathers in gms, and W is body weight of the bird in gms. This equation is based on Wetmore's (1936) data, which did not include values for sturnids. It is also interesting to note that mynas in this geographic region have more feathers as a percent of body weight (9.4%) than do starlings (7.0%). Mynas also have more feathers than starlings if calculations are based on total surface area: 4.6 and 3.2%, respectively, for mynas and starlings.

Thus, the insulative quality of myna plumage seems to be inferior to that of starlings. These differences are significant and since they cannot be explained on the basis of plumage weight, some more subtle factors may be involved.

Measurements of plumage quality using the techniques described above are inferior in that they do not measure the actual changes in plumage posture which the bird initiates when exposed to different temperatures. Possibly the use of a helium environment during metabolism experiments could essentially produce a featherless bird. A technique

has been tried and found successful by Morrison and Rosemann (personal communication) in small mammal work in which they replace the normal N_2 environment (approximately 80% of room air) with He; the diffusivity of the warmed gas in the dead air spaces increases dramatically, and the animal cannot thermoregulate. Thus, by exposing the two species to a common cold temperature in an He environment which essentially renders them featherless, metabolic rates obtained would be those representing a live featherless bird; these rates could be compared against similar rates obtained in the normal N_2 environment and both of these rates could be compared between the two species.

It is apparent that in many of the components of their life histories, the two species perform differently. The subtropical myna is found to be less well adapted to the climatic and phenological characteristics of the area of southwestern British Columbia in which it became introduced than is the common starling which introduced itself. The summary effect of all the differences already exposed, probably supplemented by others not yet studied, has led to the greater effectiveness of the starling in its new environment. At the same time the myna is successful in that it has survived here for some 80 years, the last 12 of which have been in competition with an expanding

starling population. Possibly behavioural features related to niche selection are responsible for survival of the myna despite its apparent inability to achieve thermal adaptation of the kind found in the starling.

SUMMARY AND CONCLUSIONS

1. The nesting season for starlings was synchronized into definite peaks of nest building, egg laying, hatching and fledging, which was not the case for crested mynas.
2. Clutch and brood sizes were higher in starlings than mynas. Starlings successfully reared more (38%) second broods than mynas (9%).
3. Egg transplant and heater nestbox experiments indicated that the poor nest attentiveness and low incubation temperatures maintained by crested mynas, resulted in a low hatching and consequent low fledging success.
4. Starling resting metabolism was higher than that observed for mynas.
5. During metabolism experiments at temperatures below 0°C, adult mynas did not maintain positive heat balance.
6. Active mynas housed outside at cold temperatures have higher energy requirements than starlings under the same conditions.
7. Cooling experiments indicated myna plumage was not as effective an insulator against cold as starling plumage.

Ideas formulated early in this research were concerned with the reasons for the poor colonizing success by Sturnus cristatellus cristatellus compared to Sturnus vulgaris vulgaris, both introduced to North America in the 1890's. It was hypothesized that differences in thermal adaptability might be influencing factors.

The most important factor supporting my hypothesis was the low hatching success caused by poor nest attentiveness and incubation success by crested mynas compared to both the starling living in the same environment and the closely related common myna living in West Bengal, India. A low hatching success for crested mynas in Vancouver was first described by MacKay and Hughes (1963: 158-159).

These results suggest that mynas have not adapted an incubation rhythm necessary for higher hatching success in the Vancouver environment. This is apparent when one compares the nesting success of Vancouver crested mynas with that of the tropical common myna and its similar poor nest attentiveness but extremely high hatching success (98%) in the tropics.

Resting metabolism in mynas does not deviate significantly from the expected values for birds of similar weight, however, adult and nestling myna metabolic response

to decreasing temperature is slower than that observed for starlings.

Experiments indicated myna plumage was inferior to that of starlings, and although mynas did suffer during cold periods, some birds seem to have adapted special behavioural traits to compensate for cold.

Nestling mynas were supplied more low energy content vegetable foods than starlings and the rate of food consumption and G.E. intake was lower than for nestling starlings. Subsequently nestling myna growth was slower than starlings occupying the same environment.

Although the above factors do support the original hypothesis, some factors have not been investigated that could be important. The effects of human disturbance on crested myna nesting activities have not been fully studied. Possibly starlings were simply more tolerant of disturbances near the nest, and therefore were more nest attentive when disturbances (including biological investigations) occurred during the incubation period.

An increase in the myna population to a high of approximately 20,000 birds in the late 1920s indicated a more successful population increase than observed in this study. However, this initial increase and subsequent decrease is the general trend for species invading new

habitat (Elton 1958), and a similar pattern has been observed for starlings in eastern North America. The original increase in myna numbers came at a time when the agricultural districts near Vancouver were being developed. A similar pattern of starling population increase exists for Europe (Delvingt 1961). This suggests that the initial increase in sturnid population both in North America and Europe might have been related to increased feeding areas (agricultural districts). Peak myna numbers were observed in the mid-late 1920s and early 1930s, long before any myna-starling competition was possible. Starlings had hardly spread from eastern North America by 1930 (See Figure 1). However, it still remains evident that the population has not exhibited the dramatic successful colonization that has been evidenced by starlings.

Field observations made clear the fact that mynas were aggressive during the nesting period; experienced breeders readily ejected other species from former nest sites, however little is known of competitive relationships of yearling mynas seeking nest sites for the first time. Similarly, little is known of possible competition between B.C. sturnids and other passeriform species. Competition certainly cannot be eliminated as a factor

regulating growth of the sturnid population in the lower mainland, however, a comprehensive study of such competition is not within the scope of this study.

General interpretation of results pertaining to energetics theory should be given consideration here as they seem paradoxical in many instances. In true homeotherms, heat production should equal heat loss, or the opposite, thereby having minimal affect on body temperature. During cold stress, animals lose heat at a faster rate through conduction, convection, radiation and evaporation, and heat production is therefore increased.

It is interesting to note that heat production by mynas (cal/gm-hr) is lower than that of starlings at the same cold temperatures. This would suggest, if we follow the above equation, that mynas either (1) lose less heat to the environment (better insulation) or (2) they are not truly maintaining a constant body temperature. Other experiments suggested that myna plumage was inferior to that of starlings for conserving heat; this eliminates insulation as a factor and Table 1 shows that mynas did not maintain homeothermy at cold temperatures.

At 40°C, the LD₅₀ for experimental mynas had been reached. It seems paradoxical that a bird of subtropical origin tolerates warm temperatures less well than one

introduced from a temperate environment. Possibly recent adaptations to the cold environment by mynas may have reduced tolerance at the other end of the temperature spectrum. Or possibly, at 20% relative humidity, mynas could not tolerate the evaporative water loss (not measured); but then unless starlings have evolved special physiological or behavioural adaptations, why then should they be better able to tolerate high heat and water loss?

It would seem clear that a bird which evolved in a tropical ecosystem would have a higher LCT (lower critical temperature) than one originating from a temperate climate. However, the myna LCT is not different from that of starlings.

Mynas and starlings have been in North America only about 80 years. The amount of change, morphologically, physiologically, or behaviourally (all of these under genetic control) is questionable.

The morphological changes that have occurred in house sparrows (*Passer domesticus*) since introduction in 1850, indicate the type of rapid evolution that can occur in birds in a relatively short time period (Selander and Johnston, 1967; Johnston and Selander, 1964 and 1971). The data in this thesis on myna clutch size indicate that an evolutionary change may already have occurred in this trait in the Vancouver area. The data also indicates that nest attentiveness is under severe selective pressure and yet there does not appear to have been an evolutionary response.

It seems obvious that the tropical myna incubation rhythm has changed little; similarly, mynas exhibit a slow growth rate, also typical of many tropical species. These two factors, along with the behavioural adaptations associated with relatively cool Vancouver winters, indicate that North American crested mynas have not evolved a complete new life style, but still retain many traits of subtropical origin. It is truly unfortunate that little physiological research has been done on any resident tropical birds.

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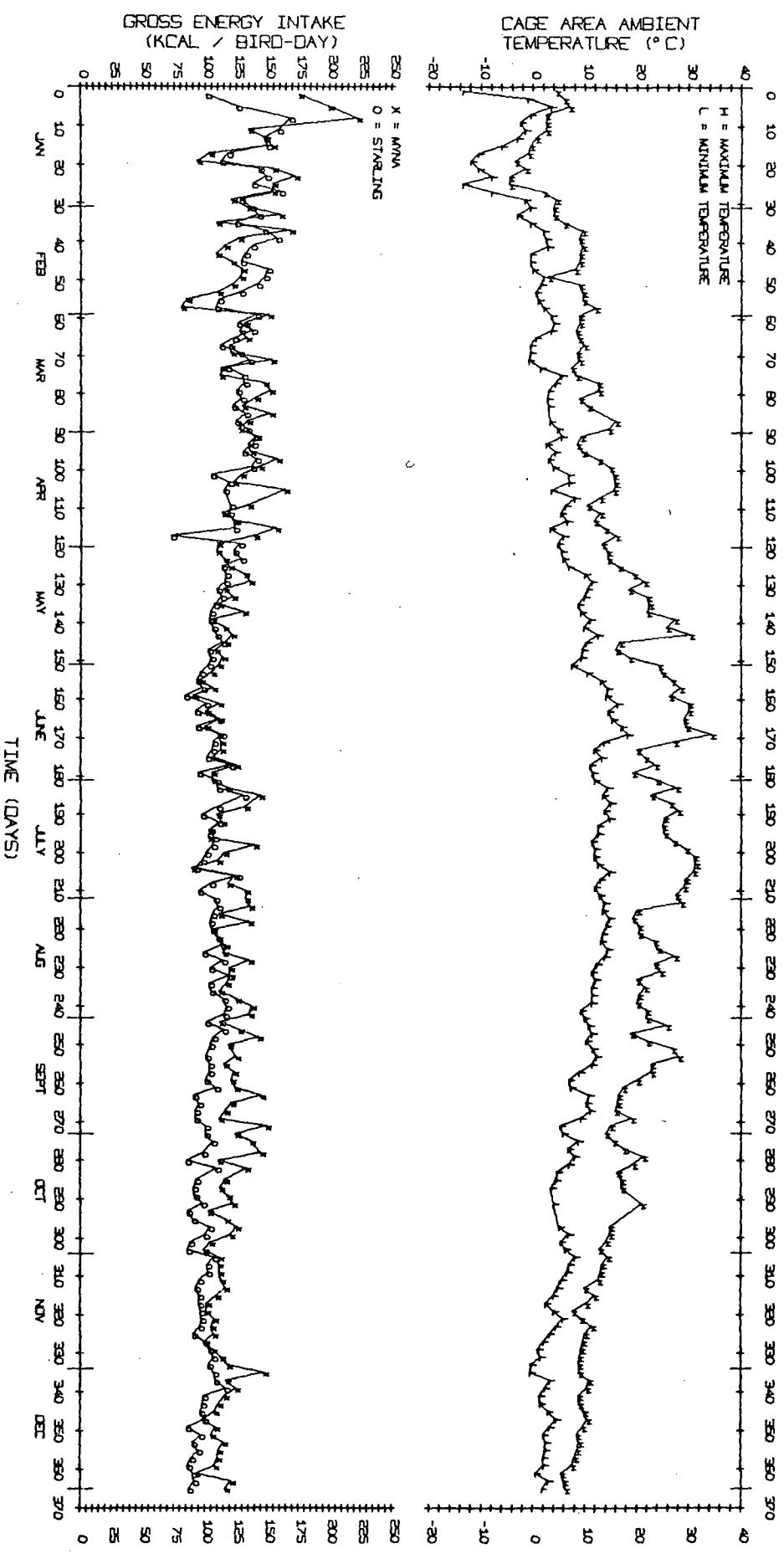
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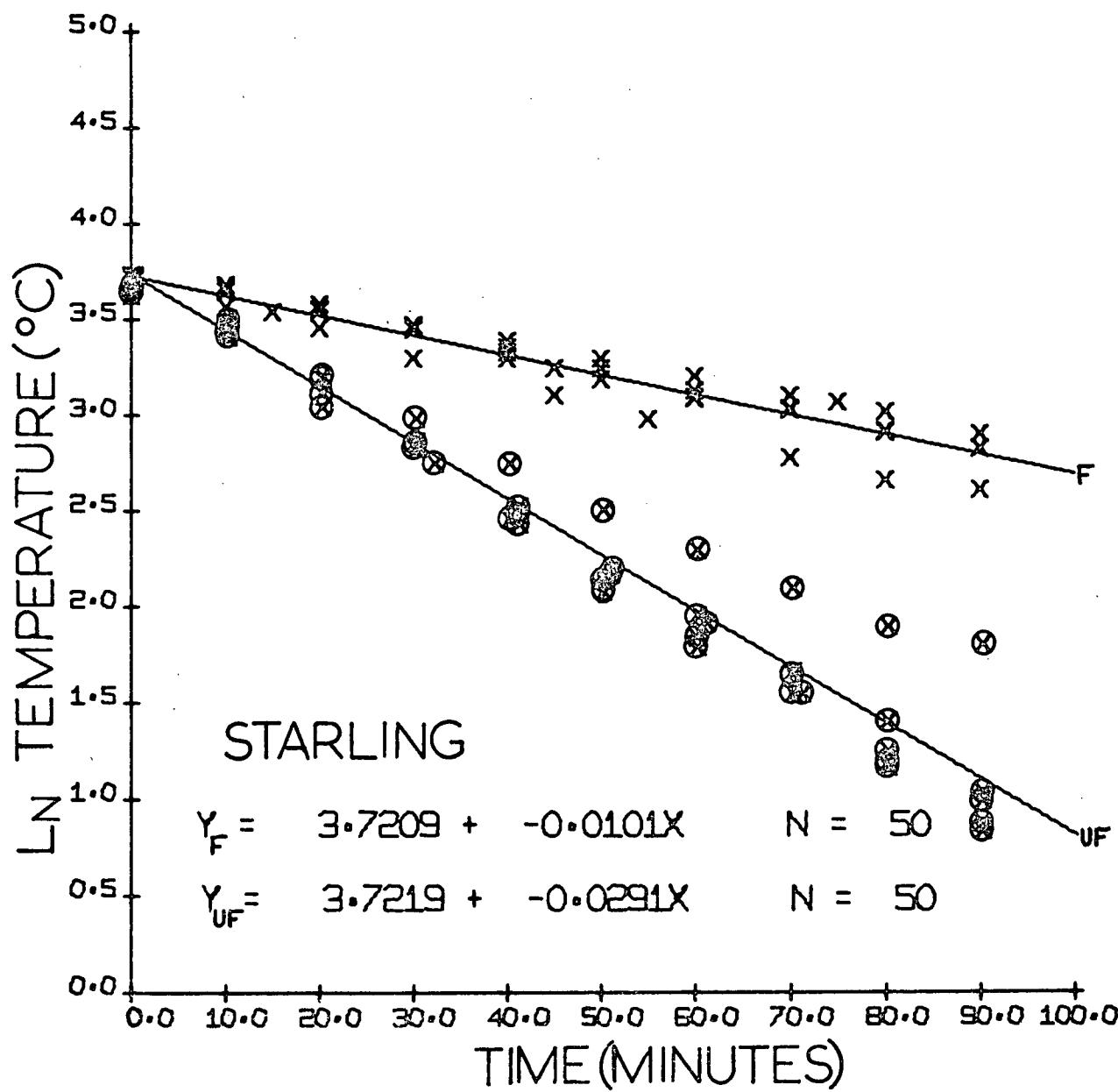
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APPENDIX

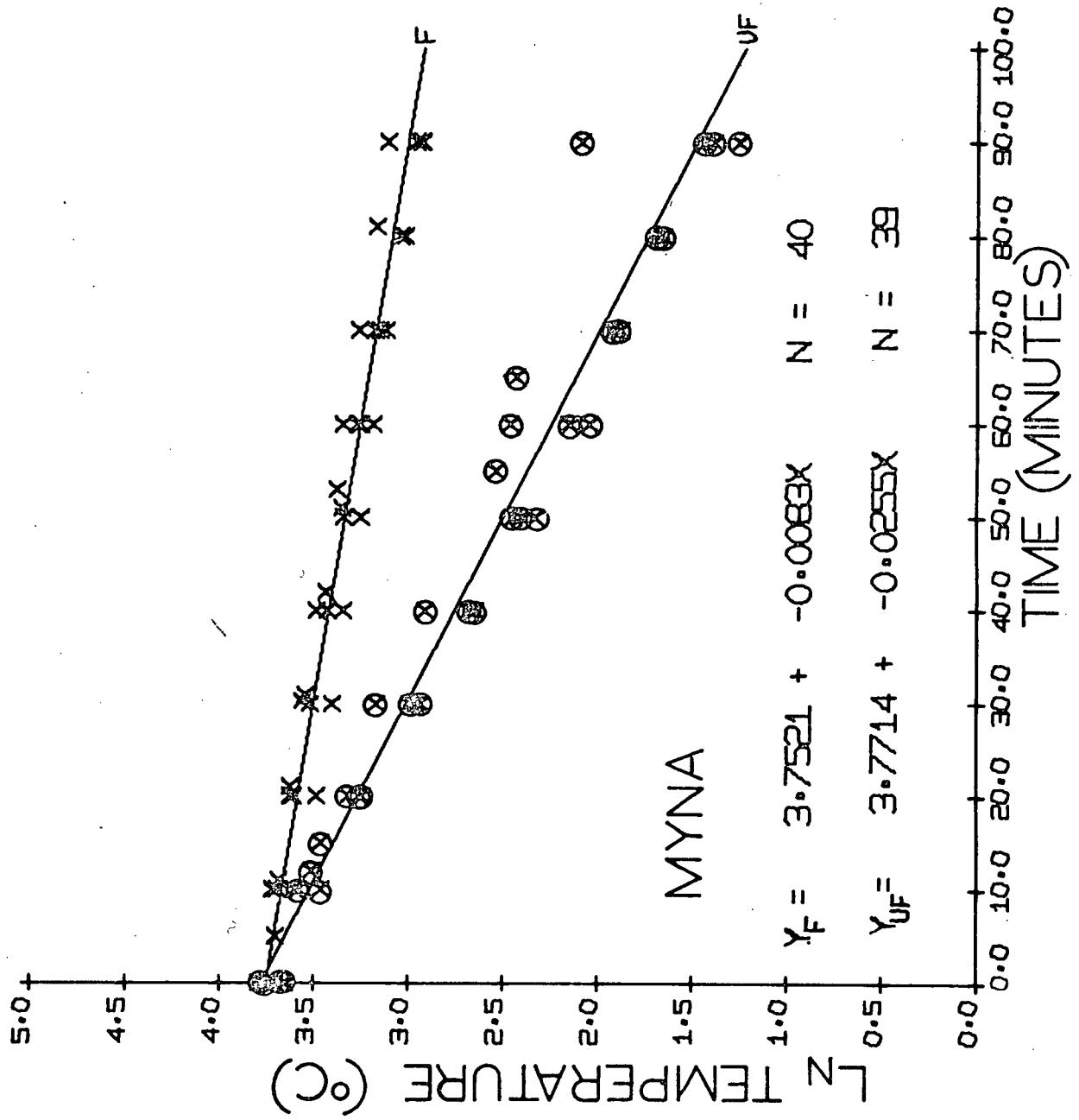
Appendix Figure 1. Computer plot of mean cage area ambient temperature ($^{\circ}\text{C}$ maximum and minimum) and sturnid G.E. intake for the period 1 January 1969 to 1 January 1970.



Appendix Figure 2. Plot of heat loss from feathered
(f) and unfeathered (uf) starling
carcasses cooled at 0°C.



Appendix Figure 3. Plot of heat loss from feathered (f) and unfeathered (uf) myna carcasses cooled at 0°C.



Appendix Table 1. Meteorological Data for Lower Mainland Areas, British Columbia, 1969

Experimental Cage Area Vivarium, UBC				UBC Weather Station						Vancouver International Airport					
Month	Temperature (°C)			Temperature			Precipitation (cm) ¹			Temperature			Precipitation		
	Mean	Max.	Min.	Mean	Max.	Min.	Rain	Snow	Total	Mean	Max.	Min.	Rain	Snow	Total
Jan.	-2.1	1.3	-5.5	-2.4	0.3	-5.2	9.4	54.3	14.8	-3.0	0.0	-6.0	7.3	65.0	12.8
Feb.	4.7	8.3	1.0	3.5	6.4	0.5	5.6	2.6	5.8	3.5	6.5	-0.5	4.4	6.9	5.0
Mar.	6.4	10.3	2.5	6.3	9.6	3.0	9.8	---	9.8	6.0	10.1	1.8	9.0	---	9.0
Apr.	9.0	12.8	5.1	7.9	10.9	4.9	13.0	---	13.0	8.4	11.9	4.9	10.8	---	10.8
May	14.8	20.6	8.9	13.1	17.0	9.1	3.4	---	3.4	13.0	17.5	8.5	2.8	---	2.8
June	20.1	26.3	13.8	16.8	20.0	13.5	2.2	---	2.2	17.4	21.5	13.3	1.7	---	1.7
July	20.4	27.7	13.1	16.5	20.3	12.6	2.0	---	2.0	17.3	22.0	12.5	1.2	---	1.2
Aug	17.4	22.3	12.5	15.5	18.3	11.8	6.2	---	6.2	15.8	20.0	11.6	5.2	---	5.2
Sept.	14.9	20.1	9.6	14.1	16.7	11.5	15.7	---	15.7	14.1	17.6	10.6	14.0	---	14.0
Oct.	11.4	16.8	5.9	10.1	13.1	7.0	10.1	---	10.1	9.6	13.4	5.8	10.4	---	10.4
Nov.	7.4	10.7	4.0	7.1	9.4	4.9	9.4	---	9.4	6.5	9.4	3.6	9.9	---	9.9
Dec.	5.4	8.6	2.2	5.6	7.4	3.8	17.7	---	17.7	5.2	8.0	2.4	15.4	---	15.4

¹ 10 cm snow = 1 cm rain

Appendix Table 2. Results of an analysis of variance on energy balance data.

GROSS ENERGY:

Calculated monthly constants presented in an ordered array (Kcal/bird-day)												
<u>March</u>	<u>Jan.</u>	<u>April</u>	<u>May</u>	<u>Aug.</u>	<u>Feb.</u>	<u>July</u>	<u>Sept.</u>	<u>Nov.</u>	<u>June</u>	<u>Oct.</u>	<u>Dec.</u>	
<u>18.62</u>	<u>14.37</u>	<u>8.23</u>	<u>4.91</u>	<u>0.12</u>	<u>-0.57</u>	<u>-1.04</u>	<u>-1.68</u>	<u>-7.54</u>	<u>-9.97</u>	<u>-11.00</u>	<u>-14.44</u>	

1

Mean standard error of difference between two months = 7.09

Mean standard error of difference between two species = 2.74

F value for months = 4.41* with 11 and 372 d.f.

Calculated species constants: Starlings Mynas

F value for species = 6.74* with 1 and 372 d.f.

(Kcal/bird-day) -4.37 +4.37

Calculated estimate of mean: 114.29

(Kcal/bird-day)

FECAL ENERGY:

Calculated monthly constants presented in an ordered array (Kcal/bird-day)											
<u>March</u>	<u>April</u>	<u>Oct.</u>	<u>Jan.</u>	<u>May</u>	<u>Aug.</u>	<u>July</u>	<u>Dec.</u>	<u>June</u>	<u>Feb.</u>	<u>Sept.</u>	<u>Nov.</u>
<u>13.08</u>	<u>8.09</u>	<u>3.26</u>	<u>2.93</u>	<u>2.63</u>	<u>1.78</u>	<u>1.60</u>	<u>-2.28</u>	<u>-3.15</u>	<u>-3.25</u>	<u>-8.11</u>	<u>-16.53</u>

Mean standard error of difference between two months = 3.51

Calculated species constants: Starlings Mynas

Mean standard error of difference between two species = 1.36

(Kcal/bird-day) +0.24 -0.24

F value for months = 12.45* with 11 and 372 d.f.

Calculated estimate of mean: 58.64

F value for species = 0.12 with 1 and 372 d.f.

(Kcal/bird-day)

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Appendix Table 2 (continued). Results of an analysis of variance on energy balance data.

METABOLIZED ENERGY

Calculated monthly constants presented in an ordered array (Kcal/bird-day)

<u>Jan.</u>	<u>Nov.</u>	<u>Sept.</u>	<u>March</u>	<u>Feb.</u>	<u>May</u>	<u>April</u>	<u>Aug.</u>	<u>July</u>	<u>June</u>	<u>Dec.</u>	<u>Oct.</u>
11.45	8.99	6.43	5.57	2.63	2.27	0.14	-1.60	-2.66	-6.80	-12.16	-14.27

Mean standard error of difference between two months = 5.30

Mean standard error of difference between two species = 2.05

F value for months = 3.82* with 11 and 372 d.f.

Calculated species constants: Starlings Mynas

F value for species = 15.82* with 1 and 372 d.f.

(Kcal/bird-day) -4.62 +4.62

Calculated estimate of mean: 55.64

(Kcal/bird-day)

¹ Values joined by solid lines are not significantly different from each other

* Designates significance ($P = .10$)

Appendix Table 3. Results of a regression analysis of temperature against G.E., E.E. and M.E. for starlings.

	Correlation Coefficients (Product moment r)	Regression Coefficients (b in Y = bX+a)	N
Temperature vs. G.E.			
Total Year	0.28	-0.49	12
Jan.-June	0.56	-0.68	6
July-Dec.	0.79	+0.88	6
Temperature vs. E.E.			
Total Year	0.00	-0.03	12
Jan.-June	0.10	-0.09	6
July-Dec.	0.53	+0.75	6
Temperature vs. M.E.			
Total Year	0.45	-0.46	12
Jan.-June	0.78	-0.59	6
July-Dec.	0.12	+0.14	6

Appendix Table 4. Results of a regression analysis of temperature against G.E., E.E. and M.E. for mynas.

	Correlation Coefficients (Product moment r)	Regression Coefficients (b in Y = bX+a)	N
<hr/>			
Temperature vs. G.E.			
Total Year	0.25	-0.48	12
Jan.-June	0.50	-0.12	6
July-Dec.	0.66	+0.89	6
Temperature vs. E.E.			
Total Year	0.10	-0.11	12
Jan.-June	0.29	-0.31	6
July-Dec.	0.56	+0.56	6
Temperature vs. M.E.			
Total Year	0.27	-0.37	12
Jan.-June	0.63	-0.83	6
July-Dec.	0.18	+0.31	6

THE INFLUENCE OF BODY SIZE ON METABOLIC RATE

Wallgren (*Acta Zool. Fenn.*, 84:110 pp., 1954) discussed the practical and theoretical aspects of expressing results of avian metabolic experiments (pp. 14-15) in terms of either $W^{1.00}$, $W^{.75}$, $W^{.67}$, or some other function of body weight (W). Since the mean live weights of the two sturnids mentioned herein were relatively similar (Myna $W=107.8 \pm .12$ gms, $n=152$; Starling $W=83.3 \pm .09$ gms, $n=189$), as were the two species studied by Wallgren, and since non-significant weight variations were observed in the experimental birds tested, my metabolic data are presented primarily in the form of $\text{cal/gm}^{1.00} - \text{hr}$. It should be mentioned however, that at the time of Wallgren's work, insufficient avian (more specifically passeriform) metabolic data were available to construct detailed linear regressions relating \ln metabolic rate to \ln body weight (W).

In the last 20-25 years more avian metabolic rates have been described and as a result relationships between metabolism and body weight have been made more clear. The most recent series of such equations are those presented by Lasiewski and Dawson (*Condor* 69:12-23, 1967).

Appendix Figure 4 compares metabolic rates of adult S. vulgaris and S. cristatellus based on their respective physiological or metabolic body weights ($W^{0.724}$; based on Lasiewski

and Dawson's (Op. Cit.) equation relating metabolism to body weight in passeriform species).

No significant changes occur in my results as a result of this normalization process (except that myna metabolism at +30°C is now non-significantly greater than starling metabolism at +30°C).

Other than those by Salt (Ecol. Monogr. 22:121-152, 1952), Wallgren (Op. Cit.), Lasiewski (Physiol. Zool. 36:122-140, 1963) and this study, few comparative energetic studies of closely related species have been conducted. In all of these studies and, in fact, in the majority of avian metabolic work, results have been expressed in terms of $W^{1.00}$.

However, it remains apparent that in any comparative study of avian metabolism, body size must be considered as an influence, and it could be argued that comparative data should be based on metabolic or physiological weights.

A more complex problem exists when comparisons are made between different weight classes of growing or developing birds. Comparisons of metabolic rates for developing altricial and precocial birds presents an even more complex problem to the experimenter because of possible different reactions of the two types of ambient temperature changes.

Appendix Figure 4. Sturnid thermal response curves expressed in terms of $\text{cal/gm}^{\frac{724}{T}}\text{-hr}$. LCT designates empirically obtained value for lower temperature (Kleiber, 1965: 165) (\circ = starling; \circ = crested myna).

