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The **North American Bluebird Society** announces the **third annual grants in aid** for ornithological research on cavity-nesting species of North America with emphasis on the genus *Sialia.* Presently, up to three awards totaling $3,000 are made annually and include the Bluebird Research Grant, available to student, professional, or individual researchers for a research project focused on any of the three species from the genus *Sialia;* General Research Grant, available to student, professional, and individual researchers for a research project focused on a North American cavity-nesting species; and Student Research Grant, available to full-time college or university students for a research project focused on a North American cavity-nesting species. Guidelines and application materials are available from **Theodore W. Gutzke, Research Committee Chairman, P.O. Box 121, Kenmare, North Dakota 58746 USA.** Completed applications must be received by **31 January 1986**; decisions will be announced by 15 March 1986.

The **Hawk Mountain Sanctuary Association** is accepting applications for its **ninth annual award for raptor research.** To apply for the $750 award, students should submit a brief description of their research program (5 pages maximum), a curriculum vitae, and two letters of recommendation by **30 September 1985** to **Stanley E. Senner, Executive Director, Hawk Mountain Sanctuary Association, Rte. 2, Kempton, Pennsylvania 19529 USA.** The Association's board of directors will make a final decision late in 1985. Only students enrolled in a degree-granting institution are eligible; both undergraduate and graduate students may apply. The award will be granted on the basis of a project's potential to improve understanding of raptor biology and its ultimate relevance to conservation of North American raptor populations.

# ENERGY INVESTED IN REPRODUCTION BY THICK-BILLED MURRES (*URIA LOMVIA*)

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ABSTRACT.—Pelagic seabirds that lay single-egg clutches have been thought to invest less energy in reproduction than inshore-feeding species that rear more than one young. To examine this idea I calculated time and energy budgets for Thick-billed Murres (*Uria lomvia*) breeding at two large arctic colonies and compared their energy expenditure with that of a hypothetical group (shirkers) that was capable of feeding at the same rate but did not attempt any reproductive activity. The difference in energy investment between breeders and shirkers was strongly dependent on the average foraging range. I also compared my results with similar estimates for inshore-feeding Black Guillemots (*Cepphus grylle*). For the two Thick-billed Murre colonies, energy allocated to reproduction represented 30% and 24% of total energy expenditure during the breeding season. These values exceed the estimates for Black Guillemots. The amount of energy invested by Thick-billed Murres at the colonies considered probably is similar to that invested by other seabirds laying larger clutches and rearing heavier young. *Received 8 December 1983, accepted 3 July 1984.*

THE allocation of resources to reproduction, as a fraction of total energy budgets, has been regarded as an important component of life-history strategy (Cody 1966, Gadgil and Solbrig 1972, Goodman 1974, Wiens and Scott 1975, Dunn 1979, Hails and Bryant 1979). Techniques for quantifying such investment vary (Calow 1979). Previous studies of seabirds have depended mainly on estimating the energetic cost of egg production and chick rearing, although the authors acknowledged that the additional flying and feeding involved in reproduction must add significantly to the total energy cost (Wiens and Scott 1975, Dunn 1979).

Oceanic seabirds, which lay small clutches and have slow-growing chicks, have been thought to make a relatively small investment in reproduction compared with most birds (Dunn 1979), and hence considered to fall at the "K" end of the r-K strategy continuum (Goodman 1974). The assumption implicit here is that smaller clutches and slower-growing chicks indicate a lower annual energetic investment by the parents. This in turn is assumed to increase their residual reproductive value by increasing survival and the number of subsequent breeding attempts.

To examine the amount of energy invested by a long-lived pelagic seabird with a single-egg clutch, I calculated the cost of reproduction for the Thick-billed Murre (*Uria lomvia*), an arctic-nesting alcid that feeds, during the breeding season, on fish and crustacea obtained mainly in offshore waters (Bradstreet 1980, Gaston and Nettleship 1981).

I adopted a new approach to calculate the amount of energy expended on reproduction. The energy expenditure of breeding birds was compared with that of a category of nonexistent birds that hypothetically lived in the same area and had the same food-collecting ability as the breeders, but made no effort to breed. I have coined the term "shirkers" for this group to distinguish them from the true nonbreeding population, which carries out many activities associated with breeding (flying to and from the breeding colony, occupying breeding sites) and therefore makes some investment toward reproduction in future years. My intention was not to test the predictions of r- and K-selection theory, but to demonstrate that our ideas of "reproductive investment" may depend heavily on the way in which we choose to measure it.

To provide some material for comparison, I estimated the reproductive investment of Black Guillemots (*Cepphus grylle*) in the same way. This is an inshore-feeding species that breeds in the same area as Thick-billed Murres, normally lays two eggs, and frequently rears two chicks.

## METHODS

Information on time budgets and foraging ranges of Thick-billed Murres was drawn from data accumulated during Canadian Wildlife Service studies on the large colonies at Prince Leopold Island, N.W.T. (86,000 pairs, 74°02′N, 90°00′W; Gaston and Nettleship 1981) and Digges Island, N.W.T. (180,000 pairs, 62°34′N, 77°43′W; Gaston et al. 1985). Data on Black Guillemots were obtained at Nuvuk Islands, N.W.T. (62°23′N, 78°05′W; Gaston et al. 1985, Cairns unpubl. data) about 25 km from the murre colony at Digges Island. Calculations of energy budgets are based on the energetics model used by Furness (1978).

*Time budgets.*—Information on time budgets was obtained during 24-h watches carried out every 5–10 days from before laying until most chicks had left, on study plots where the position of each breeding site was mapped and numbered. Thick-billed Murres incubate and brood continuously, so one member of each breeding pair was always present on each site. The arrival of the other member of the pair was marked by a recognizable greeting display (Gaston and Nettleship 1981), and the timing of arrivals and change-overs was recorded at all sites. The frequency of change-overs/24 h was used to estimate the mean number of visits to the colony by each bird.

*Foraging range.*—Information on distances traveled away from the colony was obtained from aerial surveys carried out during the chick-rearing period at Prince Leopold Island (Nettleship and Gaston 1978) and during the incubation and chick-rearing periods at Digges Island (Gaston et al. 1985, Gaston unpubl. data). Additional information for the prelaying and incubation periods at Prince Leopold Island was obtained from helicopter surveys of important feeding areas conducted by Bradstreet (1979).

*Energy expenditure for breeders.*—To calculate the energy expenditure of adult murres, their daily activities were divided into five categories:

(1) Time spent occupying the nest site, including incubation, brooding, and guarding the chick ($T_i$). Typically, birds occupying sites sat immobile; they sometimes slept. Preening and interacting with mates or neighbors occupied less than 10% of the total time. The duration of this behavior was determined by direct observation.

(2) Time spent in flight traveling between the colony and the feeding area ($T_t$). This was estimated from mean foraging range ($L$), flight speed ($S$), and mean number of visits made to the colony ($V$) using the equation $T_t = 2VL/S$.

(3) Time spent flying between different locations within the feeding area ($T_a$). Most murres seen during aerial surveys were flying either toward or away from their colonies; hence, movement between feeding areas appears to be small. I estimated 0.33 h/day, adopted as a constant, for all classes of birds throughout the season.

(4) Time spent resting ($T_r$). I could not estimate what proportion of time away from the colony was spent resting. Birds relieved at the nest site usually flew to the water close to the colony to bathe and rest. Numbers on the water sometimes amounted to as much as 10% of the entire breeding population. Some time on the feeding grounds also may be spent resting. The time during which both members of a pair were present at the site simultaneously amounted to less than 1 h/day and declined as the season progressed, suggesting that less time could be spared for rest in the chick-rearing period than during incubation. I therefore estimated time spent resting during daylight as 2 h during the incubation periods and 1 h during chick rearing. At Digges Island, where darkness imposes inactivity for a period, I assumed that one member of each pair was resting during darkness ($T_n$) and that the other was on the colony. I assumed that nonbreeders and shirkers spent the dark period resting.

(5) Time spent feeding ($T_f$). The remainder of the day I assumed was devoted to feeding. Hence, $T_f = 24 - (T_i + T_t + T_a + T_r)$.

Energy expenditure was calculated for each category, using estimates based on equations given by Kendeigh et al. (1977; hereafter referred to as KDG) and observed mean weights (900 g for Prince Leopold Island and 936 g for Digges Island). The rate for $T_t$ and $T_a$ was assumed to be the same. Because birds occupying sites ($T_i$) were inactive, I considered their rate of energy expenditure equivalent to the mean of Standard and Existence Metabolism (KDG: Eqs. 5.15 and 5.35, Table 1). For resting during daylight ($T_r$), which included bathing and other maintenance activities, I assumed a rate equal to Existence Metabolism (KDG: Eq. 5.35). Birds resting away from the colony during darkness were assumed to have the same rate of energy expenditure as for incubation ($T_i$). Expenditure in flight ($T_t$, $T_a$) was calculated from KDG Eq. 5.43. The resulting approximation (11.3 × BMR) is close to the rate measured for a 1,026-g American Black Duck (*Anas rubripes*), a bird with a rapid, flapping flight similar to that of a murre (Berger et al. 1970), but well below the rate predicted by Pennycuick's (1969) formula for the power requirements of a bird of the murre's dimensions. Details of input parameters are given in Appendix 1.

Estimates for energy expenditure during feeding present a problem because murres feed by pursuing prey underwater, using their wings for propulsion. For the Mallard (*Anas platyrhynchos*), Prange and Schmidt-Nielsen (1970) found the maximum rate of energy expenditure required for swimming was only one-third of that used in flight. However, the duck was using only its leg muscles for propulsion. In the case of the murres, because of the type of muscular activity involved, we may anticipate a rate of energy expenditure similar to that for flight. Between dives, which lasted 1–2 min, murres spent a similar length of time on the surface, usually being fairly inactive. I therefore estimated energy expenditure while feeding as 6 × BMR, which is about half the rate of expenditure in flight. This is 3.7 × SMR for a 900-g bird, which is within the range of the 2–4 × SMR

TABLE 1. Rates of energy expenditure used in calculating daily energy budgets for Thick-billed Murres at Prince Leopold Island (PLI) and Digges Island (DI).

| | Brooding/ incubation $(e_i)$[a] | Flying $(e_t, e_a)$ | Resting $(e_r)$ | Feeding $(e_f)$ |
|---|---|---|---|---|
| Energy expenditure (kcal/h) for body wt of 900 g (PLI) | 6.151 | 36.420 | 7.003 | 19.338 |
| Energy expenditure (kcal/h) for body wt of 936 g (DI) | 6.286 | 37.430 | 7.154 | 19.902 |
| Multiple of BMR | 1.9 | 11.3 | 2.2 | 6.0 |

[a] Also resting away from the colony at night.

estimated by Kooyman et al. (1982) for King Penguins (*Aptenodytes patagonica*). Their estimates presumably included some resting time. Final estimates for energy expenditure on different activities are given in Table 1.

Calculations of energy expenditure assume an ambient temperature of 0°C. At Prince Leopold Island, the mean air temperature for the entire season was very close to 0°C. At Digges Island it was 8°C, but the sea water, on which murres spent about half of their time, was constantly about 0°C, so the approximation probably remains valid.

Additional energy expended by the female in producing the egg and by both sexes in incubating was calculated from KDG Eqs. 5.51, 5.52, and 5.56. However, the cost of incubation estimated in this way was less than 2% of daily average energy expenditure, and it therefore has been ignored. Energy expended in catching food for the chick was introduced by adding the energy content of fish delivered to chicks to the estimate of total energy consumed and then using this figure to calculate the rate at which energy was captured during feeding (feeding time being constant). The cost of transporting meals and lifting them to the nest site was considered negligible.

The general equation used to calculate average daily energy expenditure (ADEE) was:

$$\text{ADEE (kcal)} = T_i e_i + (T_t + T_a)e_a + T_r e_r + T_f e_f + x, \qquad (1)$$

where $T$ = time (h), $e$ = rate of energy expenditure (kcal/h), and $x$ represents daily expenditure on egg production. Expressing all $e$'s in terms of BMR, this is equivalent to:

$$\text{ADEE (kcal)} = 3.22\,[1.91T_i + 11.30(T_t + T_a) + 2.17T_r + 6.00T_f] + x \qquad (2)$$

for a 900-g bird.

The rate at which food is captured ($R$) can then be calculated from the total energy expenditure and the time spent feeding:

$$R = \text{ADEE}\,(K + Y)/T_f, \qquad (3)$$

where $K$ = a constant representing the efficiency with which the bird converts food energy to output energy and $Y$ = the amount of food fed to the chick (kcal/day). I assumed a value of 1.18 for $K$ throughout, following Dunn's (1975) estimate for a cormorant feeding on fish.

*Energy expenditure for shirkers and nonbreeders.*—For shirkers I assumed a rate of feeding equal to that calculated for breeders at the same period and assumed that they flew only the 0.33 h required to move between feeding places. The remainder of their time I assumed was spent resting. The time spent feeding was calculated by solving the simultaneous equations:

$$0.33e_aK + T_re_rK + T_fe_fK = R_bT_f \qquad (4)$$

and

$$T_r + T_f = 23.67, \qquad (5)$$

where $R_b$ = the rate of energy intake of breeders while feeding. Hence, substituting,

$$T_f = (0.33e_a + 23.67e_r)/(R_b/K + e_r - e_f) \qquad (6)$$

and

$$T_r = 23.67 - T_f. \qquad (7)$$

Because nonbreeders did not occupy fixed sites on the colony and were not marked, I could not determine time budgets for these birds by observation. I have estimated their time and energy budgets using the following assumptions:

(1) The most capable nonbreeders could achieve a feeding rate equal to that of the breeders without the additional cost of egg formation and incubation.

(2) The least capable nonbreeders were barely able to maintain their condition in the breeding area at the median date of laying (i.e. all their time was spent feeding, except the basic 2 h for resting and 0.33 h for flying).

(3) The mean feeding rate for nonbreeders was the median value for the most and least capable.

(4) The ratio of the mean feeding rate of nonbreeders to that of breeders remained constant over the season.

(5) Nonbreeders visited the colony only once every two days.

(6) The rate of energy expenditure of birds on the

colony was equal to $e_r$ (EMR) rather than $e_i$ because they spent more time than breeders moving about and interacting with other birds (Gaston and Nettleship 1981).

Because the time budget is fixed except for time spent on the colony ($T_i$) and time spent feeding ($T_f$), these two parameters can be derived from the simultaneous equations:

$$T_i e_i K + (T_t + 0.33) e_a K + 2 e_r K + T_f e_f K = R_{nb} T_f \quad (8)$$

and

$$T_i + T_f = 21.67 - T_t, \quad (9)$$

where $R_{nb}$ = median rate of energy intake of nonbreeders while feeding and $T_t = L/S$, where $L$ is the same as for breeders.

The assumption that nonbreeders did not travel to and from the colony as often as breeders rests on the hypothesis that their fitness is maximized by maximizing the amount of time spent on the colony. Because traveling involves a high rate of energy expenditure, they should try to minimize the amount of traveling that they do. The lowest rate of exchange of breeders observed was 0.5 visits/day, so I assumed that nonbreeders maintained this schedule throughout the season at both colonies.

*Observed values for parameters.*—Observers were present at Prince Leopold Island from the start of the season in 1976. Birds were seen at the colony for the first time ($D_1$) 50 days before the median date of laying ($D_e$), but for the first 20 days after $D_1$ numbers never exceeded 25% of the breeding population. From 30 days before $D_e$, 7 1-2-day peaks of about 50-80% attendance alternated with periods when numbers were low. The mean number counted at the colony during the 30 days prior to median laying was 40% of the total breeding population. Once laying had begun, however, 50% of the breeders nearly always were present. During incubation the rate of changeovers at Prince Leopold Island rose from 1 to about 2 changes$\cdot$egg$^{-1}\cdot$day$^{-1}$ between $D_e$ and median hatching. At Digges Island the corresponding figures were 0.5 and 0.8 changes$\cdot$egg$^{-1}\cdot$day$^{-1}$. During the chick-rearing period food was delivered to chicks 3-5 times daily ($\bar{x} = 4$) at Prince Leopold Island and twice daily at Digges Island.

The number of birds attending both colonies declined from about the median date of chick departure onwards, so that less than 10% of breeding sites were occupied 2 weeks later. During this period a marked diurnal change in attendance suggested that the remaining birds were visiting the colony once a day.

The mean foraging range of birds from Prince Leopold Island was 110 km during the prelaying and incubation periods (Bradstreet 1979) and 56 km during the chick-rearing period (Nettleship and Gaston 1978, Gaston and Nettleship 1981). At Digges Island the mean foraging range was estimated as 100 km during both incubation and chick-rearing (Gaston et al. 1985, Gaston unpubl. data). The flight speed of Thick-billed Murres flying between their colony and feeding area is 58 km/h (Bradstreet 1982).

At Prince Leopold Island birds were active throughout the 24-h day up to the date when 50% of chicks had fledged (Gaston and Nettleship 1981). At Digges Island darkness imposed almost total inactivity for an average of 3 h during the early part of incubation, 4 h near the end of incubation, and 5 h by the middle of the chick-rearing period.

*Values adopted for energy estimates.*—During the prelaying period I considered time spent at the colony ($T_i$) and traveling ($T_t$) to be negligible up to $D_{20}$. Thereafter, I calculated the mean duration spent at the colony from:

$$T_i = \frac{\begin{array}{c}\text{Mean number}\\ \text{counted at the}\\ \text{colony } D_{20}\text{–}D_e\end{array}}{\begin{array}{c}\text{Total number}\\ \text{of breeders}\end{array}} \times 24 = 9.6 \text{ h/day.}$$

This indicates that birds averaged about 41 h at the colony at each visit.

I assumed that, on average, breeders made 7 trips from the feeding area to the colony before the median date of laying. Hence, the mean time spent traveling during the period $D_{20}$–$D_e$ can be estimated from:

$$T_t = 2VL/[58(D_e - D_{20})] = 0.89 \text{ h/day.}$$

I assumed that the rate of energy intake while feeding during the prelaying period was a little lower than that calculated for the start of the incubation period (45 kcal/day).

For the incubation period I used observed rates of exchange to calculate the frequency of visits to the colony by breeders and estimated the rate of visits by nonbreeders to be once every two days. I assumed that from the median date of fledging onwards, the mean daily energy expenditure of breeders took 16 days to fall to the level of shirkers.

Fresh egg weights averaged 96.5 g at Prince Leopold Island and 109 g at Digges Island. The mean weight of fish delivered to chicks was 12.5 g at Prince Leopold Island and 8.9 g at Digges Island (Gaston and Nettleship 1981, Gaston unpubl. data). Only one fish was delivered on each visit to the colony. I assumed an energy content for fish of 1.14 kcal/g fresh weight (Dunn 1975). Colony-specific input parameters are summarized in Appendix 2.

## RESULTS

*Energy expenditure.*—Estimated time budgets are shown in Table 2. Estimated daily energy expenditure by breeding murres based on these

TABLE 2. Time budgets used in estimating average daily energy expenditure for Thick-billed Murres ($h \cdot bird^{-1} \cdot day^{-1}$).

| | On colony | Traveling | Flying | Feeding | Resting (daylight) | Resting (night) |
|---|---|---|---|---|---|---|
| | | | **Prince Leopold Island** | | | |
| Breeders | | | | | | |
| Prelaying male | 9.60 | 0.89 | 0.33 | 7.59 | 5.59 | 0 |
| Prelaying female[a] | 9.60 | 0.89 | 0.33 | 8.08 | 5.10 | 0 |
| Early incubation | 12.00 | 1.90 | 0.33 | 7.77 | 2.00 | 0 |
| Late incubation | 12.00 | 3.79 | 0.33 | 5.88 | 2.00 | 0 |
| Chick rearing | 12.00 | 3.86 | 0.33 | 6.81 | 1.00 | 0 |
| Nonbreeders (average) | | | | | | |
| Early incubation | 11.25 | 1.90 | 0.33 | 8.52 | 2.00 | 0 |
| Late incubation | 11.25 | 1.90 | 0.33 | 8.52 | 2.00 | 0 |
| Chick rearing | 12.76 | 0.97 | 0.33 | 7.94 | 2.00 | 0 |
| Shirkers | | | | | | |
| Prelaying | 0 | 0 | 0.33 | 6.89 | 16.28 | 0 |
| Early incubation | 0 | 0 | 0.33 | 6.19 | 17.48 | 0 |
| Late incubation | 0 | 0 | 0.33 | 3.74 | 19.93 | 0 |
| Chick rearing | 0 | 0 | 0.33 | 3.96 | 19.71 | 0 |
| | | | **Digges Island** | | | |
| Breeders | | | | | | |
| Early incubation | 12.00 | 1.72 | 0.33 | 6.45 | 2.00 | 1.5 |
| Late incubation | 12.00 | 2.76 | 0.33 | 4.91 | 2.00 | 2.0 |
| Chick rearing | 12.00 | 3.45 | 0.33 | 4.72 | 1.00 | 2.5 |
| Nonbreeders (average) | | | | | | |
| Early incubation | 4.96 | 1.72 | 0.33 | 11.99 | 2.00 | 3.0 |
| Late incubation | 7.59 | 1.72 | 0.33 | 8.35 | 2.00 | 4.0 |
| Chick rearing | 7.50 | 1.72 | 0.33 | 7.44 | 2.00 | 5.0 |
| Shirkers | | | | | | |
| Prelaying | | | | | | |
| Early incubation | 0 | 0 | 0.33 | 5.20 | 15.47 | 3.0 |
| Late incubation | 0 | 0 | 0.33 | 3.46 | 16.21 | 4.0 |
| Chick rearing | 0 | 0 | 0.33 | 2.96 | 15.71 | 5.0 |

[a] During last 15 days, assuming egg formation extends over 15 days at a cost of 15 kcal/day.

time budgets ranged from 295 to 365 $kcal \cdot bird^{-1} \cdot day^{-1}$ at Prince Leopold Island and from 304 to 333 $kcal \cdot bird^{-1} \cdot day^{-1}$ at Digges Island (excluding the prelaying period, for which no data were available). Maximum rates represent 2.9 and 2.6 × SMR or 4.7 and 4.2 × BMR. Minimum rates occurred during the prelaying period and maximum rates during chick rearing (Fig. 1).

Corresponding figures for nonbreeders ranged from 306 to 395 $kcal \cdot bird^{-1} \cdot day^{-1}$ at Prince Leopold Island and from 324 to 384 $kcal \cdot bird^{-1} \cdot day^{-1}$ at Digges Island. Rates for "average" nonbreeders were higher than those for breeders at the start of the incubation period at both colonies, falling below them during the chick-rearing period (Fig. 1).

*Rates of energy intake.*—Rates of energy intake during feeding rose from 48 kcal/h at the time of incubation to 67 kcal/h during chick rearing at Prince Leopold Island and from 56 to 86 kcal/h over the same period at Digges Island. Median feeding rates estimated for nonbreeders ranged from 60 to 70% of the rates for breeders (Table 3).

*Energy expenditure by shirkers and the cost of reproduction.*—Energy expenditure by breeders and shirkers was assumed to be equal at the beginning of the prelaying period. Thereafter, the daily expenditure of shirkers decreased while that of breeders increased (Fig. 1). The minimum daily energy expenditure of shirkers was 223 $kcal \cdot bird^{-1} \cdot day^{-1}$ at Prince Leopold Island and 215 $kcal \cdot bird^{-1} \cdot day^{-1}$ at Digges Is-

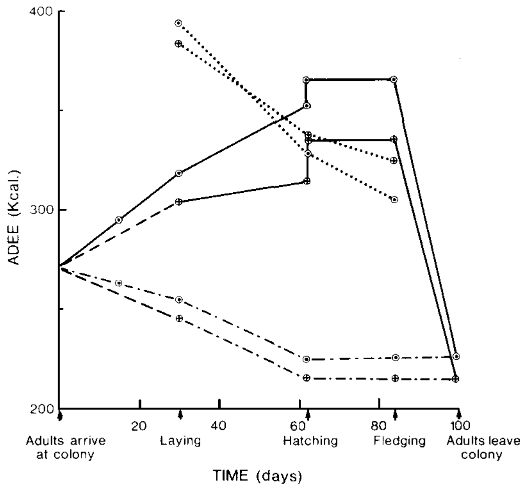

Fig. 1. Estimated average daily energy expenditure (ADEE) by breeding (solid lines), nonbreeding (dotted lines), and shirking (broken lines) Thick-billed Murres at Prince Leopold Island (circles) and Digges Island (crosses).

Table 3. Rates of energy intake during feeding (kcal/h).

| Locality/status | Start of incubation | Chick rearing |
|---|---|---|
| Prince Leopold Island | | |
| Breeder | 48.46 | 67.48 |
| Nonbreeder | 34.50 | 41.91 |
| Digges Island | | |
| Breeder | 55.71 | 85.72 |
| Nonbreeder | 39.03 | 53.39 |

land, giving maximum ratios of 1.61 and 1.55, respectively, for the energy expenditure of breeders to that of shirkers (Table 4).

I estimated the energy expenditure of breeders and shirkers over the entire breeding season by calculating the areas below the corresponding curves in Fig. 1. I then estimated the proportion of energy expenditure devoted to reproduction by subtracting the area below the shirkers' curve from the area below the breeders' curve. I expressed the difference as a percentage of the area below the breeders' curve. This yielded estimates for the proportion of energy expenditure devoted to reproduction of 30% at Prince Leopold Island and 24% at Digges Island.

*The effect of changes in body weight.*—I assumed that birds remained in energy balance throughout the season, but this assumption is not precisely correct. In one year at Prince Leopold Island and in two years at Digges Sound, Thick-billed Murres showed significant weight losses between laying and the end of chick rearing. Average weights at Digges Island in 1982 rose by 40 g between egg-laying and the middle of the incubation period (20 days) and then fell by 120 g/bird by the end of chick rearing (40 days); hence, average gains were about 2 g/day, and losses were about 3 g/day. Observations on the amount of fat present on birds collected suggested that these weight changes were caused by changes in the amount of stored fat.

One gram of fat is equivalent to approximately 9.5 kcal of energy (Pennycuick 1975, Kendeigh et al. 1977). Therefore, actual rates of energy intake in the first half of incubation may have been a minimum of 19 kcal/day greater than those predicted, and subsequent rates may have been about 29 kcal/day lower. If the food supply within foraging range of the colony remained relatively stable during this period, the observed weight gain and loss would have effectively evened out the rate of feeding necessary to support energy expenditure during reproduction.

Changes in weight also would have affected

Table 4. Sensitivity of average daily energy expenditure (ADEE) estimates for breeders and ADEE (breeder) : ADEE (shirker) ratios to variation in input parameters.

| Input parameter | Deviation of output from "best" estimate (%) | | | |
|---|---|---|---|---|
| | ADEE (breeder) | | ADEE (breeder): ADEE (shirker) | |
| | +25% | −25% | +25% | −25% |
| $e_a$ | +11 | −11 | +11 | −11 |
| $e_r$ | +1 | −1 | +19 | −13 |
| $e_f$ | +7 | −7 | 0 | 0 |
| $e_i$ | +7 | −7 | +4 | −4 |
| $L$ | +5 | −5 | +10 | −9 |
| $S$ | −5 | +5 | −9 | +10 |
| $V$ (and corresponding $Y$) | +5 | −5 | +10 | −10 |
| | 3 h | 0 h | 3 h | 0 h |
| $T_r$ | −9 | +4 | 0 | 0 |
| | 1 h | 0 h | 1 h | 0 h |
| $T_a$ | +4 | −2 | −4 | +3 |

energy expenditure, particulary in flight. Freed (1981) and Norberg (1981) have argued that weight changes during reproduction may be an adaptive response to the increased amount of flying necessitated by chick rearing. In the case of Thick-billed Murres at Digges Sound, the observed decline in weight between mid-incubation and the end of chick rearing would have altered the estimated flight energy expenditure from 40.37 to 37.82 kcal/h. Recalculating ADEE for incubation and chick rearing using the weights observed in 1982 (1,043 and 923 g) gives 395 and 363 kcal/day, a reversal of the trend in daily energy expenditure predicted assuming a constant weight.

If the changes in weight are wholly accounted for by stored fat, the difference in energy expenditure is probably less than these calculations indicate because fat deposits are likely to have little effect on BMR. Also, because the bulk of the fat is stored subcutaneously (pers. obs.), it probably helps to improve insulation and hence decrease energy expenditure on thermoregulation. The exact magnitude of the effect of weight changes on energy expenditure therefore must remain uncertain. However, heavier birds inevitably must expend more energy on flight (Pennycuick 1975).

*Sensitivity of the model to variation in input parameters.*—The effect of variation in constants derived from energy expenditure equations on a similar model was examined by Furness (1978). He found that output from his model (total energy expenditure of an entire colony) was very strongly affected by variation in these constants. My estimates of ADEE are likely to be similarly affected by these constants and should be treated with caution. However, for comparisons between breeders, nonbreeders, and shirkers, variation in the equation constants has a negligible effect because the same body weights are used for all three classes.

The ratio of energy expenditure by breeders, nonbreeders, and shirkers is affected by the relative rate of energy expenditure on different activities. To examine the sensitivity of the model to variation in the relative values of these parameters, I repeated the model calculations for the chick-rearing period with values of $e_i$, $e_a$, $e_r$, and $e_f$ that were 25% greater and smaller than my best estimates, altering the input values one at a time.

The greatest effect on the ADEE of breeders was produced by alteration of the rate of energy expenditure on flight, where a 25% variation altered the ADEE of breeders by 11%, nonbreeders by 5%, and shirkers less than 1% (Table 4). A 25% variation in the rate of energy expended while resting ($e_r$) resulted in a change of 15% in the ADEE of shirkers and hence had a big effect on the ratio ADEE (breeders) : ADEE (shirkers). Alterations in the rates of energy expended while feeding and incubating had smaller effects on outputs.

I also examined the sensitivity of the output to other input parameters. Neither time spent resting nor time spent flying in the feeding area had much effect on the output (Table 4). However, a 25% change in flight speed ($S$) or distance traveled ($L$) altered the ADEE of breeders by 5% and the rato breeders : shirkers by 9–10%.

Because foraging range ($L$) and the energetic cost of feeding ($e_f$) were poorly estimated, I examined variation in output in relation to these two parameters in greater detail, using three values for each (Table 5). Changing $e_f$ had a large effect on estimated ADEE but had little impact on the ratio ADEE (breeders) : ADEE (shirkers). Foraging range had considerable impact on ADEE for the case where $e_f$ was 10 kcal/h but a much smaller effect for the (probably more likely) cases where $e_f$ was higher. It had a large effect on the ratio ADEE (breeders) : ADEE (shirkers) for all values of $e_f$, the ratio increasing with foraging range. This is to be expected because as traveling time is reduced, a greater proportion of time is spent feeding and the energy budgets of breeders and shirkers converge, with incubation and brooding having energy demands similar to those of resting.

*Energy expenditure by Black Guillemots.*—Black Guillemots cease to brood their chicks about 5 days after hatching, and consequently they are free to feed throughout the daylight period (about 19 h at Nuvuk Islands in August) during the remainder of chick rearing. Although they make many trips to feed their chicks each day ($V$ = 5–10), they forage within 5 km of the breeding site. Hence, travel time is small compared to Thick-billed Murres. The combination of these characteristics means that, although daily energy expenditure during chick rearing is 41% greater than during incubation, the rate at which food has to be found is only slightly

TABLE 5. Average daily energy expenditure by Thick-billed Murres at Prince Leopold Island in relation to different estimates of foraging range and energy expenditure while feeding.

| | $e_f = 10$ | | | $e_f = 19.34$ | | | $e_f = 30$ | | |
|---|---|---|---|---|---|---|---|---|---|
| | Close[a] | Mid | Far | Close | Mid | Far | Close | Mid | Far |
| Incubation | | | | | | | | | |
| Breeders | 223.87 | 260.31 | 296.75 | 304.52 | 328.07 | 351.63 | 396.58 | 405.53 | 414.29 |
| Shirkers | 199.88 | 192.82 | 195.23 | 267.12 | 239.47 | 228.33 | 344.85 | 293.86 | 265.57 |
| Breeder/shirker | 1.12 | 1.35 | 1.52 | 1.14 | 1.37 | 1.54 | 1.15 | 1.38 | 1.56 |
| Chick rearing | | | | | | | | | |
| Breeders | 235.97 | 290.63 | 345.30 | 322.73 | 358.07 | 393.42 | 421.79 | 435.07 | 448.35 |
| Shirkers | 198.29 | 191.20 | 185.65 | 264.53 | 232.51 | 209.27 | 340.15 | 278.89 | 237.22 |
| Breeder/shirker | 1.19 | 1.52 | 1.86 | 1.22 | 1.54 | 1.88 | 1.24 | 1.56 | 1.89 |

[a] Average foraging ranges for the incubation period: close, 30 km; mid, 70 km; far, 110 km; and for the chick-rearing period: close, 20 km; mid, 50 km; far, 80 km.

greater during the chick-rearing period, once brooding has ceased, than during incubation (Table 6). The figures in Table 6 are based on a nest containing two chicks. For the average nest, containing 1.3 chicks, energy delivered to chicks ($Y$) is 72.8 kcal/day, and the peak rate of energy intake becomes 21.85 kcal/h, lower than that during incubation.

According to these estimates, shirkers expend practically the same energy as breeders during the incubation period, and even during chick rearing the ratio of ADEE of breeders to that of shirkers is only 1.45. These estimates are lower than the estimates for the Thick-billed Murres, although differences between the species for the chick-rearing period is largely dependent on the difference between the values I have selected for energy expended while foraging ($e_f$) and flying ($e_a$). In the terms I have adopted, therefore, the cost of reproduction seems to be lower for the Black Guillemots at Nuvuk Islands than for the neighboring Thick-billed Murres at Digges Island, amounting to only a 19% increase over the level estimated for shirkers (based on a total colony attendance period of 74 days).

## DISCUSSION

Four points deserve particular mention from these results. First, the maximum daily energy expenditure of breeding murres, at 4–5 times BMR, is high in comparison with other studies on breeding birds (Utter and Lefebvre 1973, Ricklefs 1974, Hails and Bryant 1979) and may approach the sustainable limit for birds of 4 times BMR (Utter, quoted in King 1974; Drent and Daan 1980). Measurements of energy expenditure by breeding Thick-billed Murres at Digges Island and breeding Black Guillemots at Nuvuk Islands during the incubation period using the doubly labeled water technique suggest that my estimates are approximately correct (3 incubating Thick-billed Murres, 342–421 kcal/day; 5 incubating Black Guillemots, 124–183 kcal/day; Prŷs-Jones and Gaston in prep.). In terms of SMR these estimates are also similar to those made for King Penguins (Kooyman et al. 1982), another underwater-pursuit predator.

Second, comparison with our hypothetical shirkers suggests that maximum rates of energy expenditure by breeders average 1.5–1.7 times the level that would sustain them if they made no attempt to visit the colony. Assuming that birds remain in energy balance, this suggests an equivalent increase in the amount of food consumed. The Pigeon Guillemot (*Cepphus columba*, Koelink 1972) and the Double-crested Cormorant (*Phalacrocorax auritus*, Dunn 1975), two comparable fish-eating seabirds that, on average, rear two young per nesting attempt, had estimated increases in feeding rates during chick rearing twice that of nonbreeders. Third, the estimated rate of energy intake during feeding, which during the chick-rearing period reached 3–5 times the expenditure involved, is normal, or perhaps a little higher than normal, for birds in which the young are fed at the nest (Ricklefs 1974).

Finally, the estimated daily energy expenditure of nonbreeders is not much different from that of breeders. Although this seems counterintuitive, it is quite reasonable if we assume (as the model does) that nonbreeders are

TABLE 6. Time budgets and estimates of energy expenditure for breeding Black Guillemots and shirkers.

| Status | Period | At the nest $(T_i, e_i)$[a] | Flying $(T_a + T_t, e_a)$[b] | Feeding $(T_f, e_f)$[c] | Resting, daylight $(T_r, e_r)$[d] | Resting, night $(T_n, e_i)$ | Totals (ADEE) | Rate of energy intake (kcal/h)[e] |
|---|---|---|---|---|---|---|---|---|
| Breeder | Incubation | | | | | | | |
| | Time (h) | 12.0 | 1.0 | 7.0 | 2.0 | 2.0 | | |
| | Energy (kcal) | 47.04 | 20.68 | 74.83 | 9.0 | 9.0 | 160.55 | 22.94 |
| | Chick rearing (>5 days) | | | | | | | |
| | Time (h) | 0 | 1.5 | 15.5 | 2.0 | 5.0 | | |
| | Energy (kcal) | | 31.02 | 165.69 | 9.0 | 19.60 | 225.31 | 24.38 |
| Shirker | Incubation | | | | | | | |
| | Time (h) | 0 | 0.5 | 6.93 | 12.57 | 4.0 | | |
| | Energy (kcal) | | 10.34 | 74.08 | 56.56 | 18.0 | 158.98 | |
| | Chick rearing (>5 days) | | | | | | | |
| | Time (h) | 0 | 0.5 | 6.38 | 12.12 | 5.0 | | |
| | Energy (kcal) | | 10.34 | 68.20 | 54.54 | 22.50 | 155.58 | |

[a] $e_i = 3.92$ kcal/h.

[b] $e_a = 20.68$ kcal/h, "nontravel flying" = 0.5 h.

[c] $e_f = 6 \times \text{BMR} = 10.69$ kcal/h.

[d] $e_r = \text{EMR} = 4.50$ kcal/h.

[e] $R_b = 1.18\ \text{ADEE}/R_f$ (incubation) and $(1.18\ \text{ADEE} + Y)/T_f$ (chick rearing), where $Y = 112$ kcal/day (nest contains 2 full-grown chicks).

less efficient at foraging than breeders (see Burger 1980). The extra efficiency of breeders allows them to invest time in incubation and brooding, which requires a low rate of energy expenditure compared to the additional feeding that nonbreeders must do. If nonbreeders travel from the colony to the feeding area more frequently than once every two days, as assumed by the model, then their energy expenditure almost certainly will exceed that of breeders. The possibility that prebreeders actually might be making a greater investment towards reproduction than breeders emerges, although their efforts yield no immediate output. The model estimates that nonbreeders average about 9 h/day (Digges Island) or 13 h/day (Prince Leopold Island) at the colony during the chick-rearing period. Assuming that all of this is in daylight, this suggests that half the nonbreeding population is present at any one time when we can count them. This accords fairly well with counts made at both colonies and estimates of numbers of nonbreeders as a proportion of the total population (Birkhead and Hudson 1977, Gaston and Nettleship 1981, Gaston et al. 1985).

These observations give slightly conflicting impressions of the investment in reproduction made by Thick-billed Murres, in comparison with other birds. The maximum rate of energy expenditure for most birds, however, is sustained for only a few days when the nestlings are at their peak weight (Dunn 1975). In the Thick-billed Murre feeding rates hardly vary with the age of the chick, so the maximum rate of expenditure applies for the entire 20–25-day period when the chick is being fed (Gaston and Nettleship 1981). Also, Dunn (1975) and Koelink (1972) calculated reproductive investment in a different manner, including the total energy delivered to the chicks in the adult's energy budget instead of only the energy expended on finding and catching the food. Estimated in such terms, Thick-billed Murres make a very small investment in reproduction.

If we compare the Thick-billed Murre with the Black Guillemot, we find that successful Black Guillemots at Nuvuk Islands reared an average of 1.3 chicks to fledging, with a mean fledging weight of about 350 g (Gaston et al. 1985). In contrast, Thick-billed Murres never reared more than 1 chick, and average weights at fledging at Digges Island were about 150 g. Despite this difference in reproductive output, the energy expenditure of breeders exceeded that of shirkers to a greater degree in Thick-billed Murres than in Black Guillemots during both incubation and chick rearing. Hence, the murres make a greater energetic investment than the guillemots but achieve a smaller reproductive profit.

In summary, in terms of energy expenditure, the Thick-billed Murre appears to make just as much investment in reproduction as other seabirds that have life-history strategies involving a higher potential intrinsic rate of increase. As indicated in Table 5, this conclusion depends heavily on my estimates of foraging range for the Thick-billed Murres. Although data on the foraging ranges of birds from the two colonies considered are fragmentary, additional evidence from shipboard surveys by Brown (1980) in the vicinity of Digges Island support the figures given here. The figures for close foraging range given in Table 5 are likely to be well below the mean foraging range for colonies the size of Prince Leopold and Digges islands (see also Gaston 1985). Otherwise, the results seem fairly robust to variations in input parameters within reasonable limits.

The very long distances over which Thick-billed Murres travel to find food are probably a consequence of the very large colonies in which these birds congregate (Gaston et al. 1983). This situation is typical of the species. In the western Atlantic, for instance, more than 90% of the population breeds in colonies of more than 10,000 pairs (Gaston 1980).

I conclude that the reproductive investment of seabirds appears to vary with the way that we choose to measure it. Measured by the shirker method, it probably is not closely correlated to reproductive rate. The apparently K-selected attributes of seabirds probably constitute a special case deriving from the fact that breeding sites are restricted and hence food resources for reproduction are constrained, as suggested by Ricklefs (1977).

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APPENDIX 1. Input parameters for model (energy expenditure estimates and formulae from Kendeigh et al. 1977).

| | BM (5.5)[a] | SM (5.15) | EM (5.35) | Flight (5.43) | Egg production[b] (5.51, 5.52) | Chick food[c] |
|---|---|---|---|---|---|---|
| Muliplicand | 0.5224W | 2.624W | 4.142W | 0.3157W | 2.484W | 1.14 (fish wt) |
| Exponent | 0.7347 | 0.5705 | 0.5444 | 0.698 | 0.9574 | |

[a] Formula number in Kendeigh et al. (1977).

[b] Daily investment in egg production ($x$) is estimated by dividing this result by the number of days taken to form an egg (15 days, Gaston and Nettleship 1981).

[c] Daily energy fed to chicks ($Y$) is estimated by multiplying this figure by the number of visits during the chick-rearing period ($V$).

APPENDIX 2. Summary of colony-specific input parameters (EI = early incubation, LI = late incubation, CR = chick rearing).

| | Prince Leopold Island (TBM) | Digges Island (TBM) | Nuvuk Islands (BG) |
|---|---|---|---|
| Weight (g) | | | |
| Adult | 900 | 936 | 400 |
| Egg | 96.5 | 110 | — |
| Fish | 12.5 | 8.9 | 12.0 |
| Visits·bird$^{-1}$·day$^{-1}$ ($V$) | | | |
| EI | 0.5 | 0.25 | — |
| LI | 1.0 | 0.4 | — |
| CR | 2.0 | 1.0 | 8.0 |
| Foraging range ($L$) (km) | | | |
| EI | 110 | 100 | 2 |
| LI | 110 | 100 | 2 |
| CR | 56 | 100 | 2 |
| Daylight rest ($T_r$) (h) | | | |
| EI | 2.0 | 2.0 | 2.0 |
| LI | 2.0 | 2.0 | 2.0 |
| CR | 1.0 | 1.0 | 2.0 |
| Dark period ($T_n$) (h) | | | |
| EI | 0 | 3.0 | 3.0 |
| LI | 0 | 4.0 | 4.0 |
| CR | 0 | 5.0 | 5.0 |

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On 2 April 1985 the **ICZN** gave 6 months' notice of the possible use of its plenary power in **case #2277,** published in Bull. Zool. Nomen. 42(1). Comments are invited and should be addressed to the **Secretary ICZN, % British Museum (Natural History), London SW7 5BD, England.**

*Carpophaga aurorae* Peale, 1848, and *Serresius galeatus* Bonaparte, 1855 (Aves): proposed conservation by the suppression of *Columba R. Forsteri* Wagler, 1829.

# HYBRIDIZATION, INTROGRESSION, AND MORPHOMETRIC DIFFERENTIATION BETWEEN MALLARD (*ANAS PLATYRHYNCHOS*) AND GREY DUCK (*ANAS SUPERCILIOSA*) IN OTAGO, NEW ZEALAND

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ABSTRACT.—Small numbers of Mallard (*Anas platyrhynchos*) were introduced into New Zealand from Great Britain and North America over 100 years ago. Both sexes have undergone differentiation in size and plumage characters as a consequence of hybridization with the indigenous Grey Duck (*A. superciliosa*). Pure forms of both species, as documented by early descriptions, appear to be disappearing, particularly the Grey Duck. In Otago, the Mallard and Grey Duck are introgressively hybridizing, and the majority of intergrades are Mallard-like in appearance. Separation of Mallards, hybrid birds, and Grey Ducks was achieved using a stepwise cluster analysis of mensural characters. The observed morphometric differentiation was not continuous throughout the Otago population, and a total of 5 discontinuities (groups of morphologically similar birds) were distinguished: male Mallards, female Mallards, Grey Ducks, and 2 groups of hybrid birds. The use of bivariate scattergrams of skull length and eye-lens weight provided the most useful illustration of the distinctions among Mallard, hybrid, and Grey Duck populations. As a consequence of hybridization, two morphologically distinct hybrid populations have been produced: one resembles the Grey Duck and the other the Mallard. This situation is discussed in relation to the two hybrid forms of the Marianas Mallard (*A. oustaleti*).

The Mallard was so successful in newly created agricultural habitat that by 1958 this species constituted 53% of the Mallard-Grey Duck population. Prior to 1958 the observed hybrid frequency was less than 3% and the reduction in the proportion of the Grey Duck most probably was the result of habitat reduction. In 1977 the Mallard comprised 82% of the Mallard-Grey Duck population, and there was concern over the number of pure Grey Ducks remaining in Otago. By 1981-1982 levels of hybridization, based on plumage analysis, had reached 51%, and the proportion of pure Grey Ducks had dropped to 4.5%, which is below the level suggested for the maintenance of a species. In the absence of reproductive isolation or antihybridization mechanisms between these two species, the Mallard and hybrid populations represent a potential threat to the conservation of the New Zealand Grey Duck.

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AVIAN hybridization and the phenotypes exhibited by hybrid individuals within particular areas (suture-zones: Remington 1968) and along geographic gradients have received considerable attention in recent years (Sibley 1957, Johnsgard 1960, Bigelow 1965, Wilson 1965, Short 1969, Mayr 1970, Uzzell and Ashmole 1970, Dobzhansky et al. 1977, Greig 1980, Ford 1981, Alatalo et al. 1982, Scherer and Hilsberg 1982). The rate of hybridization between introduced exotic species and closely related indigenous species, as measured by morphological change, can provide critical insight into the dynamic processes of evolution (Baker 1980). Hybridization resulting from introductions by man often is termed "unnatural" by taxonomists, but forms such as the Marianas Mallard (*Anas oustaleti* Salvadori), which is unlisted in several taxonomic treatments of waterfowl (Delacour 1956, Mayr and Cottrell 1979) because of its hybrid affinities, are of potential importance to our understanding of waterfowl evolution (Milstein 1979, Weller 1980, King 1981).

Interspecific hybrids among birds are rare, occurring at a frequency of about 1 in 50,000 individuals (Mayr 1970). Alatalo et al. (1982) suggested that many isolating mechanisms exist to select against this type of hybridization, which often "wastes genes." These mechanisms appear to be restricted in the Anatidae, for which interspecific hybridization is well documented (Gray 1958, Johnsgard 1960). Re-

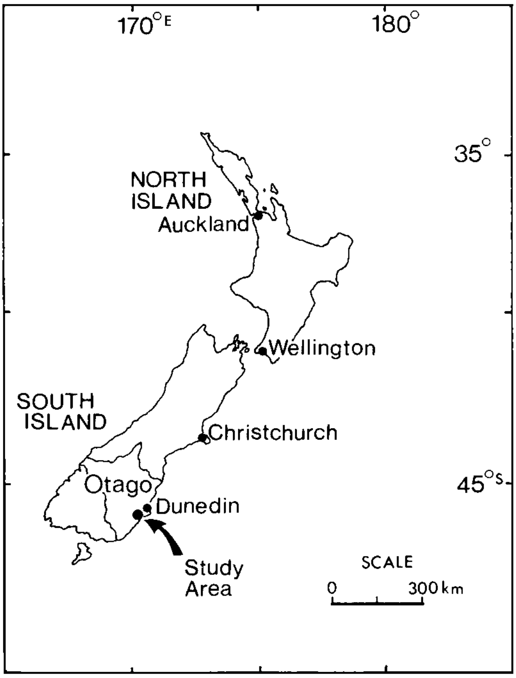

Fig. 1. Map of New Zealand showing the Taieri Plains study area where duck samples were collected. Imported Mallards were liberated in Dunedin, Christchurch, Wellington, and Auckland.

cently, Scherer and Hilsberg (1982) recorded 418 interspecific hybrids, 20% of which were fertile, which emphasizes the close taxonomic relationships of the ducks within this family.

The problem of distinguishing previously distinct species after hybridization occurs has been reported often (West 1962; Delacour 1964; Johnsgard 1967, 1975; Short 1969; Mayr 1970; Gill 1980). However, quantitative information on the degree of hybridization, the rate of morphological change, and the proportion of mixed as opposed to "pure" forms is necessary before aspects of feeding behavior, diet diversity, and competitive overlap can be studied (Alerstam et al. 1978).

In New Zealand, the taxonomy of two species of dabbling duck, the Mallard (*Anas platyrhynchos*), which was introduced in the 1860's, and the indigenous Grey Duck (*A. superciliosa*), has become confusing because of interbreeding between the two populations and the subsequent production of viable hybrid forms (Williams 1981, Haddon 1984). The earliest reference to hybridization between these species was documented by Thomson (1922), who reported that ducks shot in Christchurch in 1917 were thought to be Mallard-Grey Duck hybrids. Sage (1958), using plumage characters, estimated that the proportions of hybrids in Auckland, Wellington, Christchurch, and Dunedin (Fig. 1) were 0.3, 0.4, 4.3, and 3.0%, respectively. His figures, based on trapping returns, indicated that hybrids were more frequent on South Island than on North Island. Buchan (1977) recorded an average hybrid frequency of 6.1% (range 0.0–12.5%) based on the plumage characters of wings collected from the Taieri Plains. He suggested that the incidence of hybridization was increasing.

I present an analysis of morphometric variation in Otago populations of Mallards, Grey Ducks, and associated hybrids. An attempt was made to quantify the degree of interspecific hybridization, statistically assess patterns of variability within populations, and investigate the possible significance of the morphological differentiation exhibited among these birds.

## MATERIALS AND METHODS

All duck samples were collected from the Taieri Plains study area (Fig. 1) during the first two weeks of the 1981 and 1982 shooting seasons (May–July). First-year birds were excluded from the analyses because of obvious size variations. Yearlings were recognized by notched tail feathers (with attached down), comparatively narrow, pointed tertial coverts, the presence of a bursa (with small unsheathed penis) in young males, and a small oviduct opening (often invisible) in young females (Owen and Cook 1977, Schemnitz 1980).

The remaining birds were sexed in the field by cloacal examination (Schemnitz 1980). The head and wings of each bird were removed and placed in labeled plastic bags. All samples were frozen within 3 h of collection.

The degree of hybridization was assessed by two methods. First, a hybrid-index system was constructed based on plumage and soft-part characteristics (Anderson 1949, Johnsgard 1961, Braithwaite and Miller 1975, Hubbard 1977). Plumage categories were constructed from descriptions given for Mallards by Delacour (1956), Kortright (1962), and Palmer (1976); for Grey Ducks by Buller (1888) and Oliver (1930); and for hybrids by Sage (1958), Soper (1963), Falla et al. (1970), and Williams and Roderick (1973). Duck samples were divided into Grey Ducks, hybrids, and Mallards by allocating a score based on plumage and soft-part characters (Table 1). Ducks with scores of 0–9 were designated Grey Ducks and those with 25–35 were designated Mallards. The remaining birds, with scores of 10–24, were considered hybrids. Male and female birds were scored separately. The results were pooled and the overall frequencies calculated. Establishing absolute scores for "pure" Grey Duck (0–4) or "pure" Mallard (30–35) was difficult, even when based on direct comparisons with representative specimens and species descriptions. This may be attributable to the natural, intrinsic variation inherent in most populations (Hubbard 1977).

The second method utilized morphometric parameters and multivariate techniques in an attempt to achieve a quantitative measure of the degree of hybridization and morphological differences. Six parameters were used: (1) Wing length. The wing was flattened and measured from the flesh at the "bend" to the tip of the longest primary feather (Palmer 1976). (2) Skull length. The head was measured from the bill tip to the base of the cranium (feathers included; Owen and Montgomery 1978, Thomas 1982). (3) Eye-lens weight. The eyeballs were removed from the skull and placed in 10% formalin for 2 weeks. This soaking fixed and hardened the lenses to minimize any subsequent damage (Friend 1968, Morris 1972). The lenses were removed from the eyeball casings and left to soak for a further 4 weeks in the formalin solution. After this soaking period any ciliary material still attached to the lenses was carefully removed. The lenses were dried in a convection oven at 55°C for 48 h, placed in a desiccator to cool, and weighed on an electronic balance to the nearest 1 mg (Friend 1968, Morris 1972, Wheeler and King 1980). (4) Bill length. The bill was measured in a straight line along the dorsal surface of the exposed culmen (Baldwin et al. 1931). (5) Neck length. The neck was measured on a flat surface, but not stretched, from the base of the cranium to the junction of neck and thorax (Thomas 1982). (6) Body length. The body was measured on a flat surface from the junction of the neck and thorax to the anterior junction of the leg and body (Thomas 1982). Measurements of all characters except eye-lens weight were recorded to the nearest 0.1 mm with dial calipers or to the nearest 1 mm with a ruler.

A stepwise cluster analysis of cases, based on average linkage between merged groups (Anderberg 1973), was used to distinguish birds with similar morphometrics (Rosenberg et al. 1982). To improve the accuracy of this technique, it was necessary to choose morphologically independent parameters that would minimize the effects of age or the environment. Variations in morphological measurements were influenced by age, season, and environmental conditions (Owen and Cook 1977, Owen and Montgomery 1978). Skull length was preferable to bill length, as the exact position of the tip of the feathering often is indistinct (Owen and Montgomery 1978). Measurements of retrapped Mallards in Britain indicated that wing measurements were preferable to neck and body parameters. The elasticity of the neck and the difficulty of measuring body length accurately indicated that such measurements were useful only for comparative analyses (Owen and Montgomery 1978). Studies with Mallard and Blue-winged Teal (*Anas discors*) in the Northern Hemisphere have shown that eye-lens growth is slow, increasing linearly from hatching and leveling off at about 100 days, and continued weight changes in the eye lens, if any, are insignificant (Friend 1963, 1968). Thus eye-lens weight could be used in the analyses as an age-independent parameter, thereby minimizing the clustering of individuals of similar size with

TABLE 1. The hybrid index used for the detection of Mallard-Grey Duck hybrids (modified from Braithwaite and Miller 1975).

| Characteristic | Degree of character assessment | Value[a] |
|---|---|---|
| Face striping | | |
| Grey Duck | Two clear black stripes on a cream background | 0–1 |
| Hybrid | Obscured face stripes | 2–3 |
| Mallard | No face stripe to a thin black eye stripe in the female | 4–5 |
| Speculum borders—anterior | | |
| Grey Duck | No white bar | 0–1 |
| Hybrid | Thin white bar (2 mm) | 2–3 |
| Mallard | Broad white bar (5 mm) | 4–5 |
| Speculum borders—posterior | | |
| Grey Duck | Faint white line | 0–1 |
| Hybrid | Thin white bar (2 mm) | 2–3 |
| Mallard | Broad white bar (5 mm) | 4–5 |
| Bill | | |
| Grey Duck | Slate gray | 0–1 |
| Hybrid | Gray-yellow | 2–3 |
| Mallard | Yellow-orange | 4–5 |
| Nape | | |
| Grey Duck | Cream | 0–1 |
| Hybrid | Creamy brown | 2–3 |
| Mallard | Dark brown, varying from a dark green to a purple-green in the male | 4–5 |
| Tail | | |
| Grey Duck | Slate gray | 0–1 |
| Hybrid | Gray-brown | 2–3 |
| Mallard | Creamy brown, varying from a dark green to a purple-green in the male | 4–5 |
| Leg | | |
| Grey Duck | Gray-brown | 0–1 |
| Hybrid | Gray-yellow | 2–3 |
| Mallard | Yellow-orange | 4–5 |

[a] The index gives a score of 0 for the purest Grey Duck and 35 for the purest Mallard.

TABLE 2. The phenotypic frequencies, as distinguished by plumage and soft-part characters, of ducks collected from the Taieri Plains during the 1981 and 1982 shooting seasons.[a]

| | Scores | Sample size | Percent of total |
|---|---|---|---|
| Grey Duck | | | |
| Pure | 0–4 | 10 | 4.5 |
| Very like | 5–9 | 16 | 7.2 |
| Like | 10–14 | 18 | 8.1 |
| Hybrid | | | |
| Intermediate | 15–19 | 20 | 9.0 |
| Mallard | | | |
| Like | 20–24 | 23 | 10.4 |
| Very like | 25–29 | 37 | 16.7 |
| Pure | 30–35 | 98 | 44.1 |
| Combined categories[b] | | | |
| Grey Duck-like | 0–9 | 26 | 11.7 |
| Hybrids | 10–24 | 61 | 27.5 |
| Mallard-like | 25–35 | 135 | 60.8 |
| Total | 35 | 222 | 100.0 |

[a] Ducks were compared with typical specimens and original descriptions.

[b] Birds divided into three categories based on pooled scores.

respect to age (Humphries et al. 1981). Collection of all samples within a 2-week period minimized any seasonal differences in morphology (e.g. abrasion, molting).

The ecological implications of the various body parameters, in relation to feeding, were investigated. Skull, neck, and body measurements were summed to compare the average potential reach of Mallards, hybrids, and Grey Ducks while feeding on submerged foods (Thomas 1982). Morphological differences were tested using the Student's $t$-test with separate variances (Zar 1974); the standard deviation and coefficient of variation also were calculated. Multivariate analyses were performed on a Digital VAX/VMS computer using a BMDP program package (Dixon 1977, Hill 1979).

## RESULTS

*Discernment of hybrid birds.*—Using the hybrid-index system, samples were divided into 7 categories ranging from pure Grey Duck to pure Mallard (Table 2). The number of birds in each category gradually increased from Grey Duck to Mallard. Pure Grey Ducks, hybrids, and pure Mallards constituted 4.5%, 51.4%, and 44.1% of the total sample. However, by combining categories of like birds, it was evident that 11.7% of the specimens were essentially similar to the Grey Duck, 27.5% were variously intergrade, and 60.8% were essentially like the Mallard (Table 2). These three combined groupings were considered representative of the overall phenotypic frequency, as Mallard-Grey Duck hybrids with fewer than 5% Grey Duck or Mallard genes appear to be indistinguishable from pure Grey Ducks and pure Mallards, respectively (Williams 1970, Williams and Roderick 1973).

A range of plumage patterns was evident during analysis, especially among male and female Mallards. A total of 61 birds were identified as hybrids, and they exhibited diagnostic features of both species. Within the hybrid sample 61% of the birds were female. This higher frequency of females in hybrid populations has been reported previously (Braithwaite and Miller 1975, Hubbard 1977), although Williams (1981) maintains that many of these females are not hybrids but simply birds of variable plumage.

Skull morphology generally was similar in Mallards and Grey Ducks. A highly arched skull, smoothly curved cheeks, and a rounded lower chin were characteristic of these birds (Fig. 2). The hybrids had narrower and more elongated skulls. Braithwaite and Miller (1975) also found such elongated skulls in hybrids between the Mallard and Black Duck (*Anas superciliosa rogersi*) in New South Wales, Australia.

*Degree of hybridization.*—A dendrogram was constructed, by cluster analysis, to assess the degree of hybridization and indicate the proportion of ducks that exhibited similar morphological features. The stepwise clustering of wing, skull, and eye-lens parameters revealed a more or less steadily decreasing dissimilarity among groups (Fig. 3). Groups of ducks within this population exhibited a range of wing, skull, and eye-lens sizes that gradually increased from the smaller Grey Duck to the larger Mallard males. This progression in size of body parameters was not continuous, however; ducks of very similar morphology were evident, although the groups themselves differed substantially.

By adopting a morphological dissimilarity threshold of greater than 0.8, 5 distinct clusters of ducks with similar wing, skull, and eye-lens parameters were defined (Fig. 3). Cluster 1 was composed of 75 male Mallards and cluster 3 of 65 female Mallards. Clusters 2 and 4 contained a total of 57 hybrid birds of both sexes, and

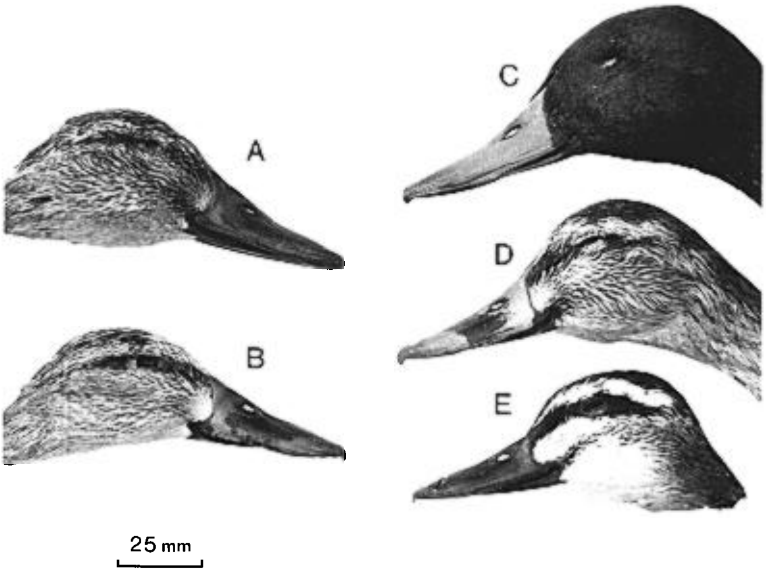

Fig. 2. Morphology of the head of hybrids, Mallards, and Grey Ducks collected from the Taieri Plains, 1981. A = male hybrid, B = female hybrid, C = male Mallard, D = female Mallard, E = male Grey Duck.

cluster 5 contained 14 male and 11 female Grey Ducks. Using these groupings, Mallards constituted 63%, hybrids 26%, and Grey Ducks 11% of the population collected from the Taieri Plains.

The similarity of individuals within the Mallard, hybrid, and Grey Duck groupings varied greatly. The most similarly clustered group was the male Mallards, with 19 (25.3%) identical individuals present (Fig. 3). In the female Mallard, hybrid, and Grey Duck groups only 18.5%, 15.8%, and 20% of the individuals were identical.

A discontinuity was evident in the clustering of hybrid individuals, and two distinct groups were present. One group resembled the Mallard (cluster 2), and the other resembled the Grey Duck (cluster 4; Fig. 3). The Mallard-like group (2) contained male and female birds that were larger in size than the males and females of the Grey Duck-like group (4). Sexual dimorphism in relation to wing, skull, and eye-lens parameters was not evident within either of the two hybrid groups.

Bivariate scattergrams of body parameters were constructed to compare the groups, as determined by cluster analysis, and to illustrate which of the three parameters was the most important in the discernment of hybrid individuals. Wing length and eye-lens weight separated the female Mallards from the hybrids and Grey Ducks. Male Mallards were separated from Grey Ducks, but there was considerable overlap between all 5 groups (Fig. 4A). Wing length and skull length, on the other hand, divided the birds into 3 groups: male Mallards, female Mallards and hybrids, and Grey Ducks (Fig. 4B). Complete separation of the 5 groups was obtained using skull-length and eye-lens weight parameters (Fig. 4C). In this scattergram, skull length divided Grey Ducks and male Mallards from female Mallards and hybrids, while eye-lens weight separated the hybrids from the female Mallards. A similar pat-

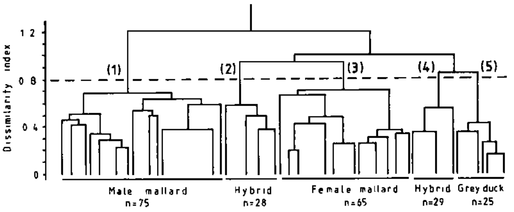

Fig. 3. Dendrogram, constructed by cluster analysis, indicating the degree of similarity of ducks collected from the Taieri Plains based on skull, wing, and eye-lens parameters. Numbers in parentheses indicate distinct clusters, as determined by the dissimilarity threshold (dashed line).

tern of morphological groups was evident in the cluster analysis, but skull length and eye-lens weight were more important than wing length in the discernment of Mallards, Grey Ducks, and hybrid birds.

*Morphological differentiation in relation to hybridization.*—Body morphology parameters within the Mallard, hybrid, and Grey Duck groups, as determined by cluster analysis, were compared. Male Mallards were significantly larger than female Mallards in all 6 body parameters (Table 3). Hybrid males had larger wing, neck, and eye-lens measurements, while the male Grey Ducks had longer bill, neck, and body measurements than their respective females.

The greatest variance in body parameters was evident among the hybrids. Eye-lens weight was particularly variable, as indicated by the high coefficients of variation for male and female hybrids (Table 3). Skull length was the most consistent measurement for all groups and had the lowest coefficients of variation.

Mallards had a longer reach and presumably are able to feed at greater depths than Grey Ducks (Fig. 5). Hybrid birds had a maximum reach that was intermediate between Mallards and Grey Ducks. Sexual differences in bill, skull, neck, and body morphology were evident in all groups. Males had the longest reach, and differences between the sexes of 16.4% for Mallards, 4.7% for hybrids, and 9.3% for Grey Ducks were recorded. Significant sexual differences were evident in the reach parameters of both the Mallards and Grey Ducks (Table 3). Mallard and Grey Duck males had longer skull, neck, and body parameters and therefore could feed at greater depths than their respective females (Fig. 5). The reduced sexual dimorphism in the reach parameters of the hybrids enabled both

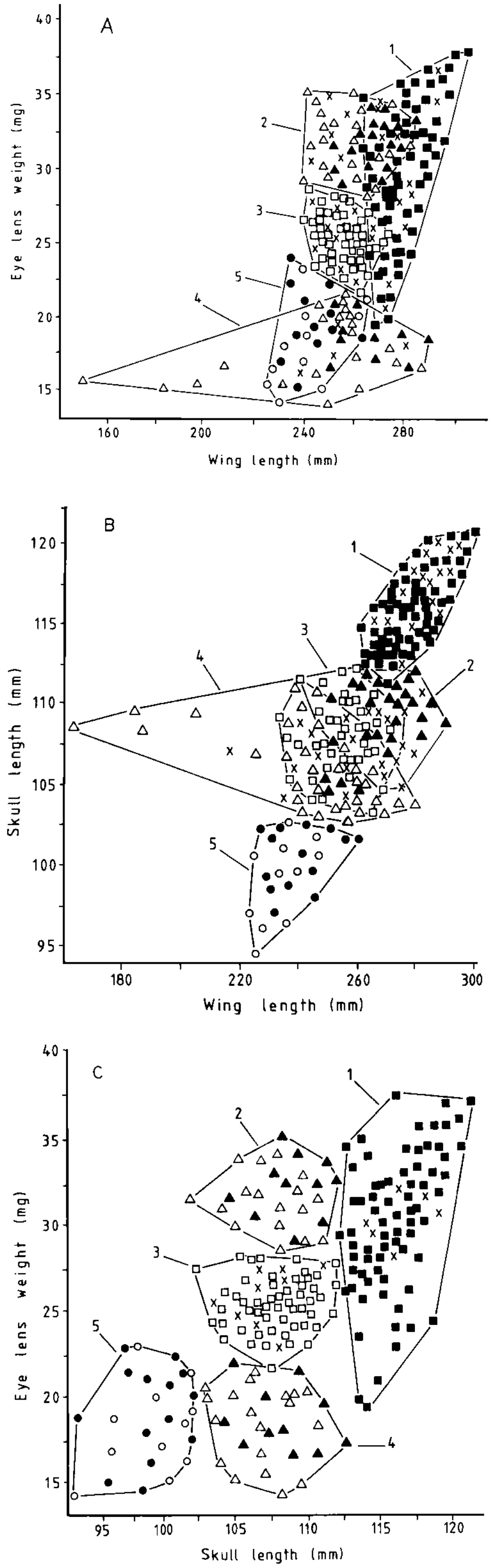

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Fig. 4. Bivariate plots of morphological measurements for Mallards, hybrids, and Grey Ducks collected from the Taieri Plains during the 1981 and 1982 shooting seasons. Lines indicate groups of individuals as determined by cluster analysis. ■ = male Mallard, □ = female Mallard, ▲ = male hybrid, △ = female hybrid, ● = male Grey Duck, ○ = female Grey Duck, X = overlap of 2 or more data points. (A) eye-lens weight and wing length ($r = 0.65$, $n = 222$, $P < 0.001$), (B) skull length and wing length ($r = 0.73$, $n = 222$, $P < 0.001$), (C) eye-lens weight and skull length ($r = 0.51$, $n = 222$, $P < 0.001$).

TABLE 3. Parameters of body morphology, as determined by cluster analysis, for Mallards, hybrids, and Grey Ducks collected from the Taieri Plains during 1981 and 1982.

| | Wing | Skull | Eye lens | Bill | Neck | Body |
|---|---|---|---|---|---|---|
| Mallard | | | | | | |
| Males ($n$ = 75) | | | | | | |
| Range | 259-298 | 111-121 | 19-37 | 48-60 | 110-231 | 171-193 |
| Mean | 275.2 | 116.3 | 30.8 | 55.1 | 222.5 | 184.6 |
| SD | 18.0 | 2.2 | 4.2 | 2.1 | 7.5 | 6.1 |
| CV[a] | 6.6 | 1.9 | 13.6 | 3.8 | 3.4 | 3.3 |
| Females ($n$ = 65) | | | | | | |
| Range | 236-273 | 103-112 | 21-28 | 47-59 | 183-201 | 138-157 |
| Mean | 254.2 | 110.1 | 24.5 | 50.1 | 194.1 | 146.2 |
| SD | 17.5 | 2.4 | 1.8 | 1.9 | 6.8 | 5.8 |
| CV | 6.9 | 2.2 | 7.4 | 3.8 | 3.5 | 4.0 |
| Value of $t$[b] | 16.97*** | 15.84*** | 11.80*** | 14.79*** | 23.49*** | 38.14*** |
| Hybrid | | | | | | |
| Males ($n$ = 22) | | | | | | |
| Range | 247-293 | 104-112 | 16-35 | 47-53 | 189-235 | 159-192 |
| Mean | 276.7 | 110.1 | 29.6 | 51.2 | 211.7 | 177.9 |
| SD | 21.7 | 3.3 | 6.8 | 3.5 | 18.1 | 12.3 |
| CV | 7.8 | 3.0 | 23.0 | 6.8 | 8.6 | 6.9 |
| Females ($n$ = 35) | | | | | | |
| Range | 143-285 | 103-111 | 14-35 | 47-54 | 164-226 | 154-193 |
| Mean | 264.9 | 109.6 | 25.8 | 50.8 | 198.8 | 172.6 |
| SD | 20.3 | 4.6 | 6.4 | 2.7 | 16.3 | 13.1 |
| CV | 7.7 | 4.2 | 24.8 | 5.3 | 8.2 | 7.6 |
| Value of $t$ | 2.05* | 0.48 | 2.10* | 0.46 | 2.72** | 1.54 |
| Grey Duck | | | | | | |
| Males ($n$ = 14) | | | | | | |
| Range | 229-263 | 96-102 | 15-24 | 46-56 | 155-174 | 139-161 |
| Mean | 248.3 | 100.7 | 20.2 | 50.1 | 165.4 | 152.5 |
| SD | 19.7 | 1.9 | 2.5 | 2.9 | 6.3 | 6.0 |
| CV | 7.9 | 1.9 | 12.4 | 5.8 | 3.8 | 3.9 |
| Females ($n$ = 11) | | | | | | |
| Range | 221-265 | 92-102 | 14-23 | 44-50 | 130-152 | 129-151 |
| Mean | 241.0 | 100.1 | 19.4 | 47.0 | 141.7 | 146.6 |
| SD | 18.8 | 1.6 | 2.2 | 1.6 | 6.1 | 6.1 |
| CV | 7.8 | 1.6 | 11.3 | 3.4 | 4.3 | 4.2 |
| Value of $t$ | 0.94 | 0.86 | 0.85 | 3.40** | 9.50*** | 2.42* |

[a] Coefficient of variation (%).

[b] Student's $t$-test, with separate variances, for male and female (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

sexes to feed at approximately the same maximum depth.

## DISCUSSION

Plumage indices and mensural characters were utilized in the discernment of Mallards, hybrids, and Grey Ducks. Cluster analysis of three independent parameters separated the ducks into 5 groups based on individuals of similar morphology. Skull and eye-lens characters were the two most important parameters in this analysis. Skull length separated Grey Ducks and Mallards, while eye-lens weight separated the hybrids. These results indicate that the degree of hybridization or range of intergrading forms is not continuous. Two distinct hybrid groups were present, and both contained individuals of both sexes. They exhibited a range of plumage patterns, but sexual dimorphism in both plumage and mensural characters was reduced considerably compared with the Mallards.

A similar situation has been documented for the Marianas Mallard. This bird also is considered to be a hybrid of the Mallard and the Grey

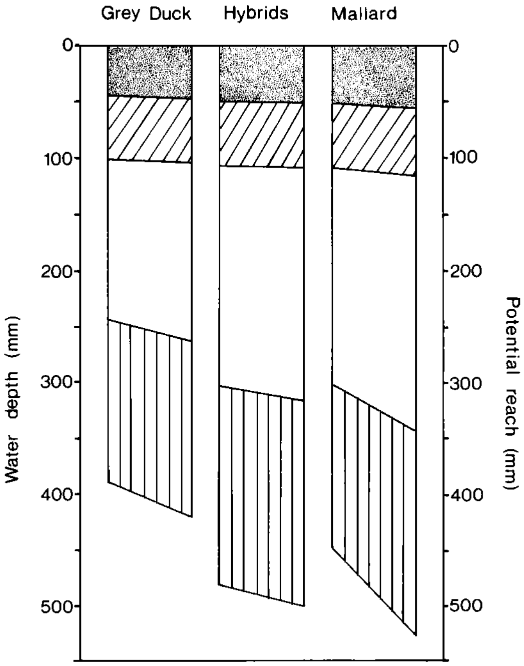

Fig. 5. Average reach morphometrics of Grey Ducks, hybrids, and Mallards in relation to feeding postures (after the method of Thomas 1982). Female measurements are given on the left of each histogram and male measurements on the right. The cumulative proportions of the various parameters are illustrated. Shaded area = bill length, diagonal lines = skull length (excluding bill), open area = neck length, vertical lines = body length.

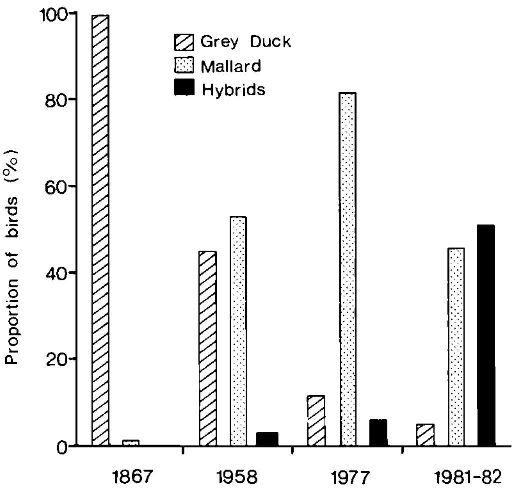

Fig. 6. The proportion of Grey Ducks, Mallards, and hybrids as determined by plumage characters in samples collected from the Taieri Plains area after the introduction of the Mallard in the 1860's.

Duck (Yamashina 1948, Amadon 1966). The literature is confusing because there are two intergrading plumage forms: one resembles the northern Mallard male in eclipse and the other the New Zealand Grey Duck (Yamashina 1948, Weller 1980, King 1981). Yamashina (1948) concluded that these two forms of the Marianas Mallard arose from hybridization of Mallards that arrived accidentally in areas inhabited by the Grey Duck. If these conclusions are correct, it appears that a similar situation has occurred in Otago, where two distinct hybrid forms also have developed as a result of hybridization between these two species.

*The significance of hybridization.*—The proportion of pure Grey Ducks in Otago has declined from 100% prior to the introduction of the Mallard in 1867 (Thomson 1922) to less than 5% in 1981 (Fig. 6). The number of Mallards in Otago appears to have increased proportionally. Buchan (1977) estimated that Grey Ducks constituted only 7.3% of the total population. This figure is a little higher than the arbitrary 5% level suggested by Short (1969) to ensure that some pure parents were present in the population and not just extreme hybrid phenotypes that appeared as pure individuals. Since 1977, levels of hybridization, which previously had been less than 3% (Sage 1958), have increased substantially from 7.2 to 51.4% (Table 2). The proportion of pure Mallards (44.1%) appears to have decreased in response to increasing hybrid levels, while the proportion of pure Grey Ducks has continued to decline (Fig. 6).

The discernment of hybrids produced between these two species is complex for a number of reasons. First, the Mallard and Grey Duck are closely related forms and probably of similar origin. This common genetic heritage may produce similar phenotypic characters at different times. Further, male hybrids beyond the first backcross (75% one species, 25% another) are often difficult to recognize because of Mallard dominance in plumage characters. Finally, female Mallard populations exhibit high levels of intrinsic variation, and the resulting forms are often difficult to distinguish from hybrid forms.

Recently, several workers have expressed concern that the New Zealand Grey Duck may be disappearing because it is hybridizing with the introduced Mallard (Weller 1969, 1980;

Dorst 1970; Greig 1980). In New Zealand, however, the attitude is somewhat different; for example, Caithness (1975) stated: "Hybridization certianly occurs but is probably confined to those areas where Greys [Grey Ducks] are persisting in low numbers on what is for them marginal habitat." Williams (1981) denied the claim that Mallards were replacing Grey Ducks through hybridization and stated: "What little evidence there is, suggests that Grey Duck are retaining their purity while Grey [Duck] blood has more strongly infiltrated the Mallard."

Introgression as described by Anderson (1949, 1953) undoubtedly occurs among the Mallard and Grey Duck populations of Otago. Three stages are necessary for this process: (1) initial formation of $F_1$ hybrids, (2) backcrossing to either of the parental groups, and (3) selection of certain recombinant types. Introgressive hybridization between the Mallard and the Grey Duck has been enhanced by the reduction of conspecific mates, the instinctive drive to reproduce, and the inevitability of forced copulations with larger, more aggressive birds. As a result, a large number of hybrid and recombinant forms now constitute a significant proportion of the population (Haddon 1984).

Whether or not the New Zealand Grey Duck will continue to exist as a distinct species under these circumstances is uncertain, but given the extremely low proportion of pure stock and the present levels of introgression, the Mallard poses a threat to Grey Duck conservation in agricultural areas. One factor necessary for a species' continued existence is reproductive isolation (Mayr 1942, Kendeigh 1961, Pettingill 1970, Dobzhansky et al. 1977). Since the Grey Duck's separation from parental stock some time in the Cretaceous (Kear and Murton 1976) and the subsequent introduction of the Mallard into New Zealand over 100 years ago, no prezygotic or postzygotic antihybridization mechanisms have developed. As a consequence, these two species hybridize extensively. The apparent genetic compatibility and hybrid fertility has produced a range of morphologically intermediate hybrid and recombinant forms (Haddon 1984).

I found significant mensural differences in the feeding morphology of Mallards, hybrid birds, and Grey Ducks. Interspecific differences in the size of the feeding apparatus often is interpreted to be a mechanism that allows two species to coexist because they can exploit foods of different sizes (Lack 1971). Differentiation in the bill, skull, neck, and body size of Mallards, hybrids, and Grey Ducks may enable the coexistence of these birds in agricultural habitats and reduce competition by partitioning available resources into different niches (Schoener 1965, 1974). At present, this hypothesis is being investigated in Otago to determine the influence of hybridization on the feeding ecology of Mallard, Grey Duck, and hybrid populations (Gillespie 1983, 1985). Further work is required to elucidate the role of hybridization as an important evolutionary mechanism inherent to waterfowl speciation.

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The **fifth edition of the *Poultry Registry of Genetic Stocks*** is now available. The price is $3.00, and copies can be obtained from **Dr. Ralph G. Somes, Jr., Department of Nutritional Sciences, U-17, University of Connecticut, Storrs, Connecticut 06268 USA.**

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The **North American Bluebird Society** announces the **third annual grants in aid** for ornithological research on cavity-nesting species of North America with emphasis on the genus *Sialia.* Presently, up to three awards totaling $3,000 are made annually and include the Bluebird Research Grant, available to student, professional, or individual researchers for a research project focused on any of the three species from the genus *Sialia;* General Research Grant, available to student, professional, and individual researchers for a research project focused on a North American cavity-nesting species; and Student Research Grant, available to full-time college or university students for a research project focused on a North American cavity-nesting species. Guidelines and application materials are available from **Theodore W. Gutzke, Research Committee Chairman, P.O. Box 121, Kenmare, North Dakota 58746 USA.** Completed applications must be received by **31 January 1986**; decisions will be announced by 15 March 1986.

The **Hawk Mountain Sanctuary Association** is accepting applications for its **ninth annual award for raptor research.** To apply for the $750 award, students should submit a brief description of their research program (5 pages maximum), a curriculum vitae, and two letters of recommendation by **30 September 1985** to **Stanley E. Senner, Executive Director, Hawk Mountain Sanctuary Association, Rte. 2, Kempton, Pennsylvania 19529 USA.** The Association's board of directors will make a final decision late in 1985. Only students enrolled in a degree-granting institution are eligible; both undergraduate and graduate students may apply. The award will be granted on the basis of a project's potential to improve understanding of raptor biology and its ultimate relevance to conservation of North American raptor populations.

Appendix 2. Summary of colony-specific input parameters (EI = early incubation, LI = late incubation, CR = chick rearing).

| | Prince Leopold Island (TBM) | Digges Island (TBM) | Nuvuk Islands (BG) |
|---|---|---|---|
| Weight (g) | | | |
| Adult | 900 | 936 | 400 |
| Egg | 96.5 | 110 | — |
| Fish | 12.5 | 8.9 | 12.0 |
| Visits·bird$^{-1}$·day$^{-1}$ ($V$) | | | |
| EI | 0.5 | 0.25 | — |
| LI | 1.0 | 0.4 | — |
| CR | 2.0 | 1.0 | 8.0 |
| Foraging range ($L$) (km) | | | |
| EI | 110 | 100 | 2 |
| LI | 110 | 100 | 2 |
| CR | 56 | 100 | 2 |
| Daylight rest ($T_r$) (h) | | | |
| EI | 2.0 | 2.0 | 2.0 |
| LI | 2.0 | 2.0 | 2.0 |
| CR | 1.0 | 1.0 | 2.0 |
| Dark period ($T_n$) (h) | | | |
| EI | 0 | 3.0 | 3.0 |
| LI | 0 | 4.0 | 4.0 |
| CR | 0 | 5.0 | 5.0 |

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On 2 April 1985 the **ICZN** gave 6 months' notice of the possible use of its plenary power in **case #2277,** published in Bull. Zool. Nomen. 42(1). Comments are invited and should be addressed to the **Secretary ICZN, % British Museum (Natural History), London SW7 5BD, England.**

*Carpophaga aurorae* Peale, 1848, and *Serresius galeatus* Bonaparte, 1855 (Aves): proposed conservation by the suppression of *Columba R. Forsteri* Wagler, 1829.

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