COMPARATIVE STUDY OF WINTER BODY COMPOSITION OF RESIDENT AND MIGRANT GREY-BREASTED SILVEREYES

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ABSTRACT.—A comparative study of the winter body composition between resident and migrant birds was made on the partially migratory Tasmanian race of the Grey-breasted Silvereye (*Zosterops l. lateralis*). Each year some members migrate from Tasmania to winter on mainland sites, while other members remain in Tasmania year-round. Resident birds were those captured at Mt. Nelson, Tasmania, during midwinter; migrant birds were those captured during midwinter at Armidale, New South Wales, 1,500 km to the north. Nighttime winter temperatures at the two locations are very similar. Both residents and migrants showed diurnal increases in lipid content, but not in other major body components. Despite differences in photoperiod and feeding conditions at the winter grounds, lipid content accumulated in the late afternoon was similar (8% of live body mass) for residents and migrants. Fractional differences in major body components between residents and migrants were negligible, being less than 0.01 in all cases. Therefore, body composition is not related to whether an individual bird is a resident or a migrant. Low night temperatures alone do not explain why the species migrate from Tasmania to places like Armidale in New South Wales. The birds could migrate for reasons such as better food conditions, higher daytime temperatures, and longer daylength for foraging on the mainland. *Received 14 January 1994, accepted 27 May 1994.*

INCLEMENT WEATHER and low food availability during winter are often implicated as the main forces in the evolution of bird migration (Cohen 1967, Berthold 1975, Gauthreaux 1982). Small passerines breeding in temperate latitudes are of special interest because they have high metabolic rates and substantial increases in rates of energy expenditure when confronted with winter cold and diminishing food supplies (Dawson et al. 1983). In order to reduce thermoregulatory costs in winter, many species have evolved adaptations that enable them to migrate to warmer regions. These include enlargement of the pectoralis muscle (Lundgren and Kiessling 1988), flying at night (Moore and Kerlinger 1991), and substantial changes in body composition leading to massive fat accumulation (Ramenofsky 1990). The latter is known as migratory fattening, which normally develops in the premigratory period in which fat stores can more than double compared with the nonmigratory period (e.g. Odum 1960, Berthold 1975, Dawson et al. 1983, Bairlein 1991). Birds that remain in their temperate breeding area in winter may reduce energy expenditure by

roosting communally (Chaplin 1982), roosting in hollows (Kendeigh 1961), adaptive hypothermia (Reinertsen and Haftorn 1986), or daily torpor (Prinzinger et al. 1991), but most bear the increased costs of thermoregulation by increasing their daily energy stores to a level greater than at other times of the year (e.g. King 1972, Carey et al. 1978, Dawson and Marsh 1986, Haftorn 1989, Blem 1990). The latter is known as winter fattening, the amount of which is particularly important because it correlates with thermogenic endurance (Carey et al. 1978, Dawson et al. 1983). Thus, sedentary and migratory birds, because they respond differently to variations in climate and food, differ in the various components of their body composition at certain times of the year.

Partial migration, in which some members of a species or a population migrate while other members do not, is a topic that has received recent interest because intraspecific variation allows insight into the evolution of migratory behavior in birds. Whether an individual is a resident or a migrant is commonly attributed to its genes or social-dominance status (Berthold 1984), although other factors (e.g. body size, habitat, intrasexual selection) have been postulated to contribute (see Ketterson and Nolan 1983, Adriaensen and Dhondt 1990, Belthoff and Gauthreaux 1991). Less emphasis has been

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placed on the relationship between variation in body composition and sedentary or migratory behavior. Because body composition is related to cold tolerance and associated food shortage, which are the main concerns of small birds in winter, the decision to migrate or not may be greatly influenced by the bird's body-composition change or augmented energy storage.

The Grey-breasted Silvereye (*Zosterops lateralis*) is a partially migratory species in which migrant individuals undertake regular north-south seasonal migration in eastern Australia (Mees 1969). In this study I compared the body composition of resident and migrant individuals of the Tasmanian race (*Z. l. lateralis*) on their natural winter grounds. The resident and migrant winter sites selected for the study experience similar nighttime temperatures, and the question why silvereyes migrate to such a place was posed.

Fig. 1. Winter range of the Grey-breasted Silvereye from Tasmania. Dark shading is breeding and winter ground; light shading is mainland winter ground. Information following Mees (1969).

MATERIALS AND METHODS

Forty-nine Grey-breasted Silvereyes were originally collected from Mt. Nelson in southern Tasmania (Fig. 1) during the austral midwinter between 25 June and 2 July 1990. These silvereyes were referred to as residents, given that any migrant birds in the region would have departed by that time of the year. One bird was later omitted from the analysis for reasons related to errors during the experimental procedure. Body mass on the same population has been studied by Chan (1994a). Thirty migrant Grey-breasted Silvereyes from Tasmania were collected from the mainland site of Armidale, New South Wales between 25 July and 1 August 1990, and between 26 June and 18 July 1991. Armidale is situated in the Northern Tablelands close to the top of the Great Dividing Range at about 1,000 m above sea level, and represents a northern wintering area for the subspecies (Fig. 1). The winter grounds of the residents and migrants have similar winter climates (e.g. average minimum of 0°C in July, similar number of days with frost), although they are 1,500 km apart. This effectively minimizes the climatic influence on the body-composition state between resident and migrant birds, although the mainland site provides longer day length and has more days with higher daytime temperatures. The Tasmanian Silvereye can be distinguished from other silvereye subspecies by a number of morphological characters (Mees 1969), but I used only those migrant silvereyes with characteristics very similar to those of the Mt. Nelson birds. This method substantially reduced errors associated with subspecific identification.

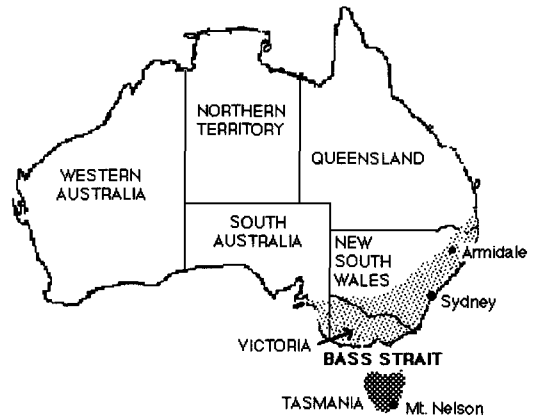All birds were captured in mist nets, and the time of capture was recorded to evaluate changes in body composition with time of day. Freshly-caught birds were weighed immediately (i.e. live mass) to the nearest 0.1 g, then killed. The gut was emptied, feathers were plucked and weighed, and the bird was weighed again (i.e. fresh mass). The carcass was dissected for gonadal and skull examination, and then frozen for later use. For analysis of body composition, each carcass was dried in an oven at 60°C until mass was constant. The dry carcass was weighed (i.e. dry mass), homogenized, and placed in a membranous thimble inside a Soxhlet lipid extractor containing a 2:1 diethyl ether-ethanol mixture. The homogenized meat was allowed to boil for 4 h, after which the residue was dried again. The solvent used in the extraction process extracts the main storage lipid, triglyceride, as well as structural fat, while little nonlipid material is extracted (Dobush et al. 1985). Water content of a bird was calculated from the difference in body mass before and after drying. Fat-free mass (lean wet mass) is obtained by subtracting the lipid amount from fresh mass. Fat-free dry mass (lean dry mass) is the dried residue after extraction, which is an accepted estimate of protein content (Dobush et al. 1985). Lipid content is the mass lost during extraction. The fat index is the percentage of lipid content in lean dry mass. The water index is the percentage water of lean body mass (following Ellis and Jehl 1991).

RESULTS

Live body mass of resident (n = 48) and migrant (n = 30) Grey-breasted Silvereyes ranged from 9.9 to 14.9 g and from 10.8 to 13.2 g, respectively. In residents and migrants, there was an increase in lipid content with time of day (two-tailed Student's t-test; residents, t = 2.02,
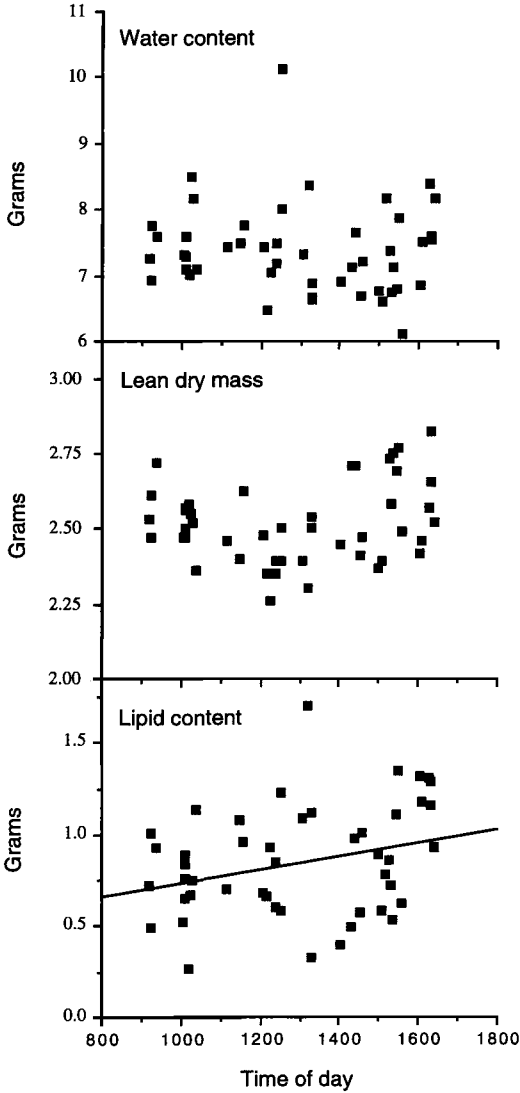
Fig. 2.   Diurnal variation in body composition in 48 resident Grey-breasted Silvereyes from Tasmania during midwinter.
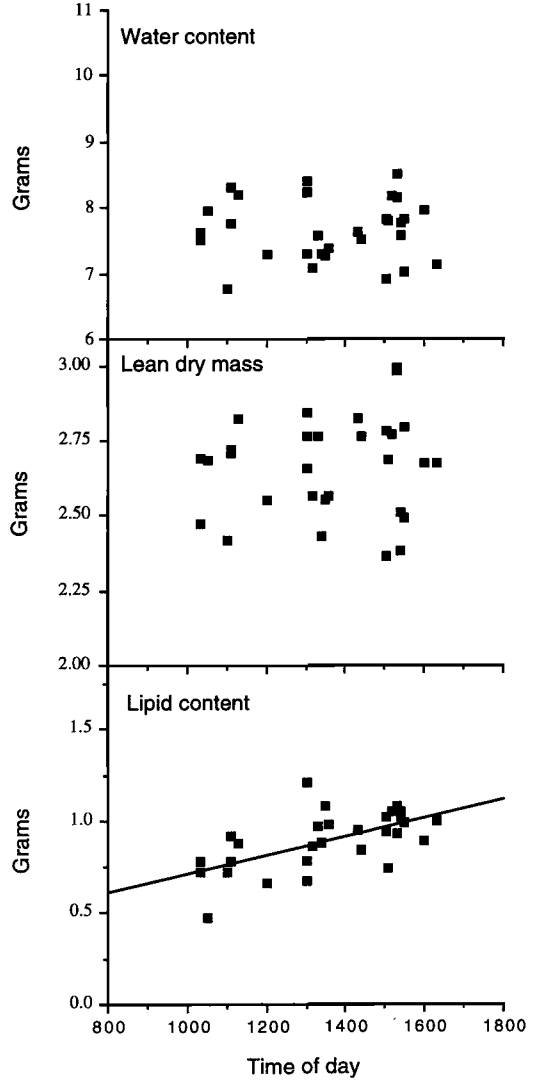
Fig. 3.   Diurnal variation in body composition in 30 migrant Grey-breasted Silvereyes from Tasmania during midwinter.

df = 47, P < 0.05, Fig. 2; migrants, t = 4.01, df = 29, P < 0.001, Fig. 3). No difference was found in lean dry mass or water content. The calculated regression equation for lipid content (L) of residents is

$$L = (3.7 \times 10^{-4})T + 0.359, \qquad (1)$$

and for migrants is

$$L = (5.0 \times 10^{-4})T + 0.215, \qquad (2)$$

where lipid content is in grams and time (T) is in hours (0900, 1000, etc.). The regression lines

did not differ between residents and migrants (F_s = 0.21, df = 1,74, P > 0.5). Lipid content of residents averaged 0.85 ± SE of 0.45 g, corresponding to 7.4 ± 0.4% of live mass, while lipid content of migrants averaged 0.90 ± 0.03 g or 7.4 ± 0.2% of live mass. Lipid content varied positively with fresh and dry mass for both residents (fresh mass, t = 6.23, df = 47, P < 0.001; dry mass, t = 13.18, df = 47, P < 0.001) and migrants (fresh mass, t = 2.09, df = 29, P < 0.05; dry mass, t = 5.82, df = 29, P < 0.001; Fig. 4).

Fifteen residents and 12 migrants were cap-

Residents

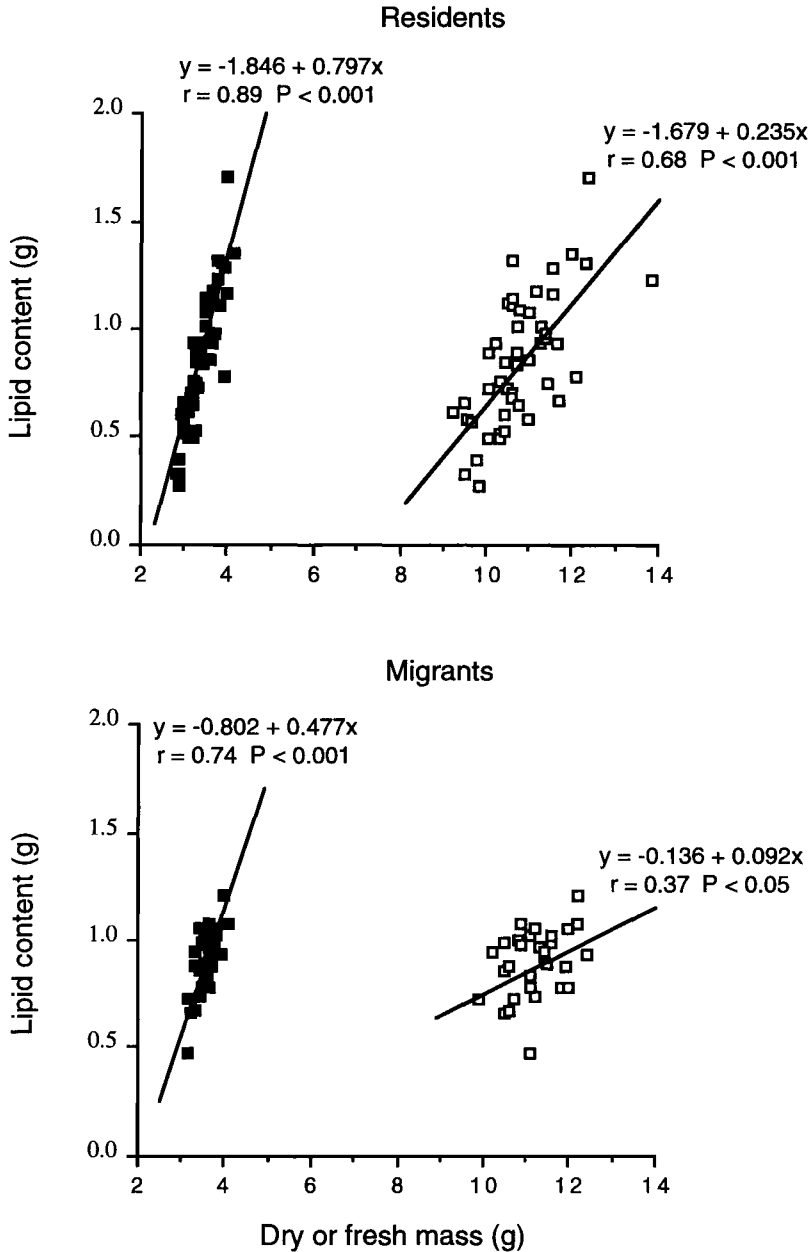## Migrants

Dry or fresh mass (g)

Fig. 4. Relationship of lipid content with dry (closed squares) or fresh (open squares) mass in resident (*n* = 49) and migrant (*n* = 30) Grey-breasted Silvereyes from Tasmania during midwinter.

tured within 2 h of sunset. Body-component values obtained from these birds are representative of amounts accumulated near the end of a day. The late-afternoon mass of residents did not differ between the sexes or between adult and juvenile birds, and a sex/age interaction was not evident (two-way ANOVA; sex, $F = 1.62$; age, $F = 0.26$; interaction, $F = 2.43$; all df = 1 and 11, $P > 0.05$). The late-afternoon mass of migrants also did not differ between the sexes or age classes (sex, $F = 0.77$; age, $F = 0.10$; interaction, $F = 0.84$; all df = 1 and 8, $P > 0.05$).

TABLE 1. Mean values ± SE (*n*) of late-afternoon body mass (g) and lipid content (g) of resident and migrant Grey-breasted Silvereyes according to sex and age.

	Sex		Age	
	Male	Female	Adult	Juvenile
Residents				
Live body mass	11.55 ± 0.38 (8)	11.99 ± 0.37 (7)	11.90 ± 0.33 (10)	11.46 ± 0.46 (5)
Lipid content	0.83 ± 0.09 (8)	1.09 ± 0.13 (7)	0.95 ± 0.10 (10)	0.94 ± 0.15 (5)
Migrants				
Live body mass	12.34 ± 0.24 (5)	12.14 ± 0.36 (7)	12.19 ± 0.26 (10)	12.40 ± 0.60 (2)
Lipid content	1.00 ± 0.03 (5)	0.96 ± 0.04 (7)	0.96 ± 0.03 (10)	1.04 ± 0.02 (2)

Lipid content also did not differ between sexes or age classes, and there was an absence of interaction for both residents (sex, $F = 3.51$; age, $F = 0.05$; interaction, $F = 0.77$; all df = 1 and 11, $P > 0.05$) and migrants (sex, $F = 0.27$; age, $F = 0.76$; interaction, $F = 0.01$; all df = 1 and 8, $P > 0.05$). Nonsignificant differences also were found for other body components; therefore, sex and age data were pooled. Table 1 shows the late-afternoon mean values of live body mass and lipid content of residents and migrants according to sex and age. Table 2 shows the late-afternoon mean values of all body components of resident and migrant birds. Although migrants in the sample were on average 0.47 g heavier than residents, none of the absolute values of the major body components were significantly different ($P > 0.05$). The fat index differed by 0.009 and the water index by 0.008. Lean dry mass of live mass differed by 0.8%, and feather content of fresh mass differed by only 0.2%. In fact, all component fractions differed by less than 0.01, and none of these were significantly different.

DISCUSSION

Winter fattening is a survival mechanism common in nonmigratory birds of the Temperate Zone (King 1972, Dawson et al. 1983, Blem 1990). Among the few studies on partial migrants, Olson and Kendeigh (1980) found that winter lipid storage of the Field Sparrow (*Spizella pusilla*) from eastern North America was double that of the summer store, while proteins and carbohydrate changed comparatively little during the same period. Blem (1981) showed that midwinter values for lipid, dry, and lean dry mass in the European Starling (*Sturnus vulgaris*) were highest in resident and migrant birds

found at the middle latitudes, rather than high and low latitudes of the eastern United States. Although these studies provided interesting data seldom reported for partial migrants, neither separated resident from migrant individuals. In a study involving captive resident and migrant populations, autumn and spring fat masses of the migratory race of the House Sparrow (*Passer domesticus bactrianus*) were high because of migration, but midwinter fat was only about one-half of that found in the sedentary *P. d. domesticus* (Dolnik and Gavrilov 1975: fig. 4). This suggests differential physiological states in winter through features associated with the development of adaptations to migration in migrant individuals, and to winter acclimatization at higher latitudes in resident individuals. In contrast, captive individuals from migratory and nonmigratory populations of the White-crowned Sparrow (*Zonotrichia leucophrys*) showed negligible differences in winter body mass, although factors associated with captivity may have disrupted winter fattening patterns in these birds (Mewaldt et al. 1968).

My work provides a rare field comparison between resident and migrant members of the same species. The winter body composition of resident and migrant Grey-breasted Silvereyes was nearly identical at the birds' respective wintering grounds, which had similar nighttime temperatures. Lipid content (but not other major body components) increased with time of day, indicating that fat is mainly responsible for the body mass daily cycle. Equivalent amounts of fat were accumulated prior to night roosting, and this amount (8% of live mass) is sufficient for an overnight's fast (Chan 1994a). The sun rises at Mt. Nelson in early July at about 0730 EST and sets at 1700. Concurrent sunrise and sunset in Armidale is roughly 0620 and

TABLE 2. Mean values ± SE of body components of resident ($n = 15$) and migrant ($n = 12$) Grey-breasted Silvereyes. All t-tests between resident and migrant birds are not significant.

Component	Residents	Migrants
Live mass (g)	11.75 ± 0.26	12.22 ± 0.22
Fresh mass (g)	10.93 ± 0.25	11.21 ± 0.19
Dry mass (g)	3.59 ± 0.09	3.65 ± 0.07
Lipid content (g)	0.95 ± 0.08	0.98 ± 0.03
Lean dry mass (g)	2.64 ± 0.05	2.67 ± 0.06
Water content (g)	7.34 ± 0.17	7.71 ± 0.14
Lean wet mass (g)	9.98 ± 0.20	10.38 ± 0.19
Lean dry/lean wet	0.264 ± 0.005	0.257 ± 0.003
Dry/live mass	0.305 ± 0.004	0.299 ± 0.004
Lipid/live mass	0.080 ± 0.006	0.080 ± 0.002
Lipid/fresh mass	0.086 ± 0.006	0.087 ± 0.003
Lipid/dry mass	0.260 ± 0.017	0.268 ± 0.007
Lean dry/live mass	0.740 ± 0.017	0.732 ± 0.007
Water/live mass	0.625 ± 0.004	0.631 ± 0.004
Water index	0.735 ± 0.004	0.743 ± 0.010
Fat index	0.358 ± 0.032	0.367 ± 0.013
Feather/fresh mass	0.075 ± 0.001	0.077 ± 0.006

1720. The fat reserve at sunset differed very little between residents and migrants, being 1.00 g and 1.08 g, respectively. The mean values for lean dry mass in the late-afternoon period also were similar at 2.64 and 2.67 g for resident and migrant birds, respectively. Rooke et al. (1986) gave a similar value of around 2.6 g for sedentary silvereyes from Margaret River (*Z. l. gouldi*) in Western Australia, in spite of the lower mean body mass (10 g) of those birds. Thus, lean dry mass in the species as a whole remains essentially stable despite changes in total body mass. The 0.735 and 0.743 water indices I obtained for resident and migrant silvereyes, respectively, also are similar to the midwinter water index of 0.73 calculated by Rooke et al. (1986) on the Western Australia silvereye population. These indices are within the range of other passerines (Skadhauge 1981, Ellis and Jehl 1991). The consistency of these findings leaves little doubt that mean winter fat, protein, and water contents in the Grey-breasted Silvereye are essentially homeostatic across individuals during winter, irrespective of whether the birds are migratory or sedentary.

By choosing to remain at their breeding ground for the winter, residents might be better adapted to the cold than their migrant counterparts. One such adaptation may be related to body size, with larger individuals more able to endure longer fasting than smaller individuals; therefore, larger individuals would be more likely to remain at their breeding ground for the winter (Ketterson and Nolan 1983). However, late-afternoon body mass of resident Grey-breasted Silvereyes in the sample was not significantly different from that of migrants. Moreover, the predictive equation calculated by Chan (1994a) from a larger sample size of the same resident population gave an estimate of 12.22 g at sunset, which is an identical value to the late-afternoon mass of migrants. Feather mass also did not differ between residents and migrants, indicating that feathers do not provide increased insulation among residents. In terms of energy storage, there was no evidence for adaptation in the major body constituents for winter survival which might result in residency.

An opposing argument is that migrant birds have a greater capacity to carry more fat than residents, as shown in the migratory period. As a result, migrant Grey-breasted Silvereyes should put on more fat when confronted with low temperatures. Certainly, migrant Grey-breasted Silvereyes possess the ability to put on excess fat during migration (Chan 1994b). However, the data suggest that the preadaptation enabling migrant silvereyes to alter their bioenergetic state for migration does not have a bearing on winter body composition. This is not surprising, since it is widely known that winter fat levels are lower than the physiological capacity attained for migratory purposes (Berthold 1975, Blem 1990, Houston and McNamara 1993). It appears that winter fattening in the resident and migrant elements reflects a response to environmental conditions. When nighttime temperatures are similar, the fat reserve of migrants and residents are also similar. This is because birds tend to carry only just above the fat amount necessary for overnight thermoregulation (King 1972).

Therefore, the data are consistent with those of Rogers et al. (1993), who demonstrated similarity in winter fattening between different populations of Dark-eyed Juncos (*Junco hyemalis*) exposed to the same local environmental conditions. In that study, fat response clearly was not a population-specific trait. In my study, winter fattening is not specific to a resident/migratory trait. Grey-breasted Silvereyes mi-

grating to mainland sites other than high-altitudinal areas, such as Armidale, would encounter higher night temperatures. Because of the lower nighttime energy demands, these birds might be expected to carry less energy reserve. For them, one reason for migration may be related to cold avoidance. For birds migrating to places like Armidale, avoiding cold does not appear to be as important.

Why, then, do Grey-breasted Silvereyes from Tasmania travel 1,500 km to winter in an equally cold place? One factor that demands attention is an analysis of the difference in photoperiod between Mt. Nelson and Armidale. Birds in the latter site experience about 1.5 h more daylight than those in Mt. Nelson. Several studies have found that increased fat levels are correlated with decreasing daylength (Haftorn 1989, Houston and McNamara 1993). No such correlation was found here because, although the resident silvereyes experienced shorter foraging time and longer overnight fasting, they did not carry greater levels of reserves. However, longer daylength allows extended foraging time. Also, solar energy and maximum temperatures at Armidale are normally higher than in Tasmania, and feeding conditions are likely to be more favorable in the former. Food supply in Australia is often unpredictable (Ford 1989), and individual physiological responses to this resource may be quite varied (e.g. Chan et al. 1990). The unpredictable nature of food supply may well be the reason why partial migration is a common occurrence among temperate birds in Australia. Although migration may be food related, the making of the decision to migrate or to stay remains a mystery. However, a recent study (Chan 1994c) showed that while some captive silvereyes are capable of developing migratory restlessness, others will only do so if actively-migrating individuals are placed in the same room, indicating a strong social influence on the decision-making. Experiments involving metabolic response to cold stress, tolerance to extreme temperatures, and tolerance to prolonged fasting are required to further evaluate whether the decision is influenced by the birds' physiological capability.

ACKNOWLEDGMENTS

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