CHAPTER 6: Body Size and Body Condition

Body mass is an easily obtained, non-invasive measure that can give immediate feedback on the health and general condition of the individual under scrutiny. It can be used to index the energy costs of specific life history events or stages, and to uncover productive avenues of investigation (Nice 1938). Sudden fluctuations in mass, especially when they are correlated with known behavioral or physiological conditions, can signal the presence of environmental stressors (Ricklefs 1974, Ricklefs and Hussell 1984) as well as altered, adaptive shifts in the regulation of appetite (Sherry et al. 1980) and of energy reserves (King and Farner 1959; King 1961a,b). In this chapter variation in wing length is related to sex and age and variation in body mass and fat class is related to reproductive status. This information is then used to pinpoint shifts in energy balance and in levels of stress as *oriantha* progressed through the complete cycle of nesting and rearing young.

WING LENGTH AND SEX

Banks (1964) found more sexual dimorphism in wing lengths of White-crowned Sparrows than in any other trait. Males were sufficiently larger than females in most populations such that this measurement could be used reliably to separate the sexes. Tioga Pass *oriantha* also exhibited this dimorphism. Wings of adult females (one-year-old or older) had a mean length of 75.67 mm (SD = 1.61 mm, min = 71 mm, max = 81 mm, N = 374), whereas mean length was 80.09 mm in adult males (SD = 1.81 mm, min = 75 mm, max = 85 mm, N = 449). This difference in means was 5.8% and highly significant (t = 37.0, $P < 0.001$). In *oriantha* captured at Hart Mountain, Oregon, the sex difference in wing length was 5.5% (Mewaldt and King 1986).

Wing lengths appeared to be normally distributed within the 1 cm range found for each sex, with some overlap between sexes occurring between 75 and 81 mm (Fig. 6.1). By themselves, therefore, they were not sufficient for determining sex in the live birds. Note that presence of a brood patch or cloacal protuberance or, if necessary, a laparotomy were used in this study to determine sex, not wing length. Nonetheless, this measure might be an effective way of determining population sex ratios if more positive means of identification were unavailable (Mewaldt and King 1986, Wheelwright et al. 1994). Wing length values might also

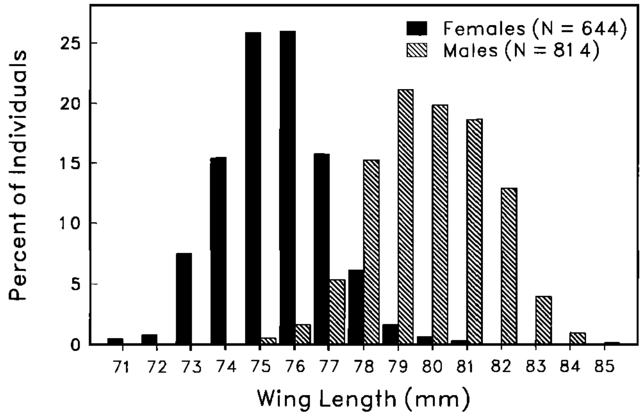

FIGURE 6.1. Frequency of wing lengths in female and male *oriantha* at Tioga Pass.

TABLE 6.1. WING LENGTHS (MM) OF *Oriantha* ACCORDING TO SEX AND AGE

	Age (yr)	Males			Females		
		Mean	SD	N	Mean	SD	N
Juveniles	0	79.49	1.57	365	75.32	1.34	270
Adults	1	79.45	1.83	258	75.29	1.66	220
	2+	80.95	1.39	191	76.21	1.36	154

be useful as morphological correlates or predictors of migration behavior, especially if data are available from members of the same species with different migrational tendencies. In White-crowned Sparrows, for example, Banks (1964) found that subspecies that migrate the longest distances (*leucophrys* and *gambelii*) have wings that are about 7–8% longer than those that are sedentary or migrate only a relatively short distance (*nuttalli* and *pugetensis*).

WING LENGTH AND AGE

Change in wing length with age is a widely observed phenomenon in passerines. Specifically, wings frequently become longer at the end of the first postnuptial (prebasic) molt. This molt usually occurs in one-year-old adults immediately following their first breeding season (Van Balen 1967) and it is the first complete molt in many species. In a study that involved relatively small sample sizes of several passerine species, Stewart (1963) found the increase in wing length to be on the order of 2–3% in males, less in females. In a large, unsexed sample of *gambelii* this increase was 1.7% (Barrentine et al. 1993), and in *gambelii* of known sex the increase was 2.3% in males and 1.5% in females (Mewaldt and King 1986). In *oriantha* the increase was 1.9% in males ($t = 9.92$, $P < 0.001$) and 1.2% in females ($t = 5.85$, $P < 0.001$; Table 6.1). These differences were derived from wing lengths obtained from one-year-old adults during the breeding season (before their first postnuptial molt) and from two-year-olds, also during the breeding season. Wing lengths of juveniles (age 0 yr) measured after their primaries had grown in and before they departed on migration are also included in Table 6.1. The data indicate that mean wing lengths in young birds had not changed by the time they returned the next summer as one-year-old adults (males: $t = 0.30$, $P = 0.759$; females: $t = 0.20$, $P = 0.842$; Table 6.1). Frequency distributions of wing lengths also had not changed (Kolmogorov–Smirnov test; males: $N_1 = 365$, $N_2 = 253$, $D = 0.065$, $P = 0.553$; females: $N_1 = 270$, $N_2 = 220$, $D = 0.092$, $P = 0.257$). Thus, there was no evidence that directional selection on wing size occurred in *oriantha* during their first winter or first two migrations, although overwinter mortality has been shown to accentuate sexual size dimorphism in House Sparrows (*Passer domesticus*; Johnston and Fleischer 1981).

Wing lengths appeared to increase slightly with age in the older birds (Fig. 6.2), but the effect was not significant (males: ANOVA $F_{7,813} = 0.73$, $P = 0.571$; females: ANOVA $F_{7,643} = 0.30$, $P = 0.910$). Van Balen (1967) also found that one-year-old Great Tits had shorter wings than older birds and that wing lengths remained constant with age beyond the time of the first complete molt. He and others have suggested that growth of remiges might be restricted in young birds for nutritional reasons, but Alatalo et al. (1984) have pointed out that the one-year-old vs. older adult wing-length dichotomy is ubiquitous and most marked in

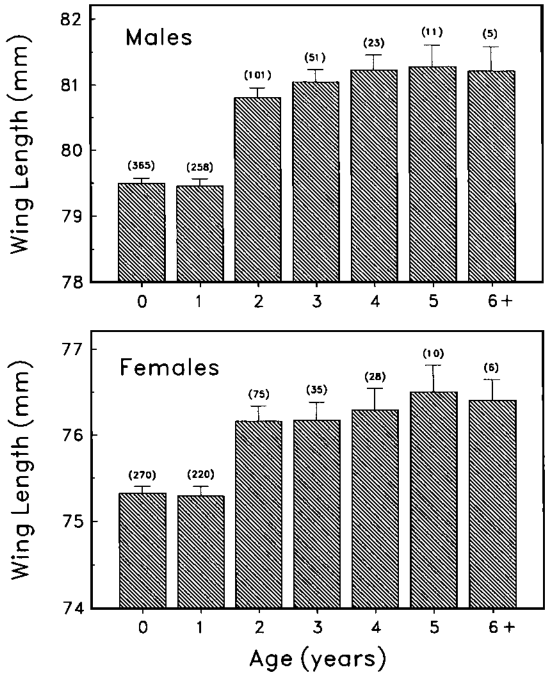

FIGURE 6.2. Mean wing length (+1 SE) in *oriantha* of various ages at Tioga Pass. Age 0 individuals were juveniles with fully grown primaries. Sample sizes in parentheses.

species that do not change their primaries in the postjuvenal molt (such as White-crowned Sparrows). They suggested that young birds have shorter wings, not because of uncompleted growth, but because short wings give them increased maneuverability. Presumably this enhances survival when birds are inexperienced and particularly vulnerable to predation. The *oriantha* wing length data can be interpreted to support this hypothesis, and so does their autumnal behavior in the days or weeks prior to migration. At that time juveniles were in flocks and we often observed them engage in vigorous aerial pursuits of one another. These flights usually included many tight turns and abrupt changes in direction. Perhaps they were gaining strength and honing evasive skills, skills that are enhanced by short wings. Once individuals have survived a year the focus of natural selection, as it bears on wing length, might then switch to other factors, such as increased flying speed or simply to a larger body size, since wing length and total mass are closely correlated (Rand 1961, Van Balen 1967).

SEASONAL CHANGES IN BODY MASS

The seasonal highs and lows of mean body mass were congruent in the sexes. Lows, which occurred in late July, were 26.9 g for males and 25.0 g for females (Table 6.2). Highs, in early October, were 33.7 g for males and 29.9 g for females. This represented a change of 25.3% in males and 19.6% in females. During May, mass decreased slightly then increased on into mid-June as the population, on average, began to prepare for reproduction. Combining the early May data into a 10-d interval obscures the interesting fact that the very first males to arrive still

TABLE 6.2. SEASONAL CHANGES IN BODY MASS (G) IN ADULT *Oriantha* AT TIOGA PASS, POOLED OVER 18 YR

	Males					Females				
	Mean	SD	N	Min	Max	Mean	SD	N	Min	Max
May										
1–10	28.3	2.0	26	25.3	33.4	26.2	1.6	7	24.2	28.2
11–20	27.8	1.3	84	25.2	30.8	25.6	1.6	33	24.2	28.3
21–31	28.8	1.6	173	25.5	32.5	26.8	2.1	133	24.0	30.7
June										
1–10	28.7	1.4	418	24.0	32.6	27.8	2.1	344	22.5	34.0
11–20	28.4	1.4	428	24.8	32.5	28.2	2.1	465	23.4	32.2
21–30	27.9	1.3	265	25.0	31.5	27.2	2.3	320	23.0	33.2
July										
1–10	27.3	1.3	218	25.0	32.0	26.4	2.5	234	22.5	35.0
11–20	27.0	1.5	285	22.5	30.6	26.2	2.6	305	22.3	34.7
21–31	26.9	1.4	261	22.5	30.5	25.0	1.7	232	21.3	34.0
August										
1–10	27.5	1.5	271	23.8	34.5	25.2	1.6	313	21.3	30.5
11–20	28.6	1.7	188	24.0	32.8	26.1	1.8	202	21.2	29.5
21–31	29.5	1.7	152	25.2	34.5	26.8	1.7	122	22.6	29.7
September										
1–10	29.6	1.8	176	25.0	33.4	27.3	1.8	135	23.0	34.5
11–20	31.8	3.1	220	26.1	39.8	27.9	2.9	204	21.8	36.5
21–30	31.6	2.8	170	26.5	39.2	29.2	3.0	187	23.5	37.5
October										
1–10	33.7	3.0	108	26.4	41.1	29.9	2.7	70	24.5	36.4

showed signs of migratory fattening. The earliest capture of a male was on 3 May and a total of five were captured before 6 May. This group had a mean mass of 31.1 g (SD = 1.3 g) whereas 21 males captured between 6 and 10 May weighed 27.5 g (SD = 1.2 g). These means were different ($t = 6.41$, $P < 0.001$), and the data suggest that hyperphagia, and the attendant obesity typical of migrants, was quickly terminated at the very end of migration. No fat newly-arrived females were ever captured, however. Male Willow Warblers (*Phylloscopus trochilus*) also arrived at breeding areas with extra fat (Fransson and Jakobsson 1998), and since the weather was usually favorable, the authors suggested that these reserves could be used for obtaining and defending a territory rather than as insurance against poor feeding conditions.

Other data of interest can also be gleaned from Table 6.2. For example, the heaviest adult male ever captured by us (in early October) weighed 41.1 g and the heaviest female (in late September) weighed 37.5 g. These individuals were obviously among those that had accumulated large amounts of fat in order to fuel their autumnal migration. Some very heavy females (34–35 g) were also present in July. These were laying females with greatly enlarged ovaries and oviducts.

Adults weighed the least from about mid-July to mid-August, with the lightest male being 22.5 g and the lightest female 21.2 g. This was also when their fat classes were lowest (Morton et al. 1973), and corresponded to the time when the majority were completing their season of parental care. When examined in the hand, many of these individuals, particularly the males, appeared to be very lean,

TABLE 6.3. FAT CLASSES IN *Oriantha* AS DETERMINED BY APPEARANCE OF SUBDERMAL FAT DEPOTS

	Fat depots		
Fat class	Claviculocoracoid	Lateral thoracic, subalar, and spinal	Medioventral, abdominal, and ischiopubic
0	None	None	None
1	None	Streaks	Streaks
2	Trace	Partially filled	Thin covering
3	Partially filled	Prominent, filled	Thick covering
4	Filled flush	Bulging	Bulging slightly
5	Bulging	Bulging	Bulging

and lacked even traces of subdermal fat (fat class = 0; Table 6.3). To find out what lean body mass actually was, we collected birds in June, weighed them, extracted their body lipids with petroleum ether in a Soxhlet apparatus, then subtracted the mass of lipid from the original body mass. Thus determined, lean body mass was 27.16 g in males (SD = 1.43 g, N = 20) and 24.59 g in females (SD = 1.46 g, N = 20). These data can be used as a reference point for judging relative leanness in live birds, plus they indicate that males were about 10% larger than females. According to information obtained with the doubly-labeled water technique, metabolic rate was about 10% higher in both males and females with nestlings than it was during the incubation period (W. Weathers et al., unpublished data). So the extremely low body mass relative to fat-free mass exhibited by adults toward the end of the parental phase suggests that some catabolism of non-adipose tissues, such as skeletal muscle, may have occurred to meet the costs of rearing young.

Mean body mass of both males and females began a steady increase in early August that continued until the last of them had departed from the study area in October (Table 6.2). During the first six weeks or so, this gain was due to restoration of tissues such as fat and muscle (Morton et al. 1973) and to an increase in blood volume that was associated with the growth of new plumage in the postnuptial molt (Morton and Morton 1990). The final portion of weight gain occurred as molt began to wane in September and was due solely to fat deposition.

To relate body mass and fat condition of *oriantha* more closely to their natural history than was possible from the data in Table 6.2, these two parameters were grouped in birds whose reproductive activities were known. Six stages or periods, each with its own biologically-coherent duration, were selected for this purpose. They covered the period from 10 days prior to ovulation to 10 days after fledging had occurred (Table 6.4).

TABLE 6.4. DURATIONS OF REPRODUCTIVE ACTIVITIES OF *Oriantha* ESTABLISHED FOR EVALUATING CHANGES IN BODY MASS AND FAT CLASS

Duration (d)	Description of activity
10	Pre-ovulating (courtship and nest building)
4	Ovulating (duration dependent upon clutch size)
12	Incubating
10	Nestlings present
20	Fledglings present
10	Post-parental (fledglings independent)

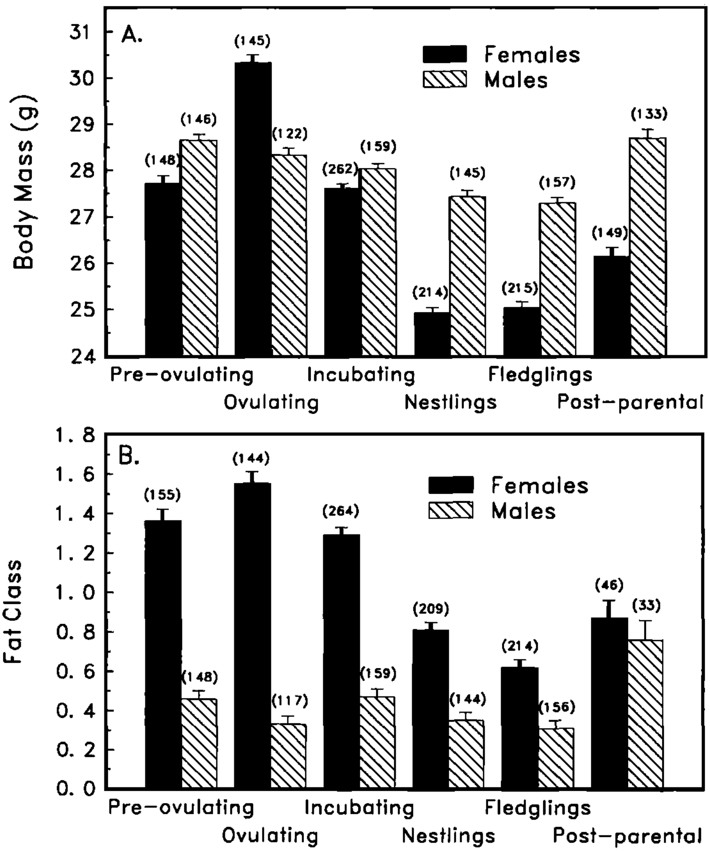

FIGURE 6.3. Mean (+1 SE) body mass (A) and fat class (B) in adult female and male *oriantha* in relation to various periods in the reproductive cycle (durations defined in Table 6.3). Sample sizes in parentheses.

Mean body mass of males (Fig. 6.3A) varied significantly between these six periods (ANOVA $F_{5,756} = 19.19$, $P < 0.001$). Their mass decreased once they began caring for nestlings (Scheffe's test, $P = 0.034$) and increased in the post-parental period ($P < 0.001$). Mean mass of females also varied significantly (ANOVA $F_{5,1027} = 211.07$, $P < 0.001$). Mass increased from the pre-ovulating period to ovulating period (Scheffe's test, $P < 0.001$), decreased from ovulating to incubating ($P < 0.001$), decreased again when they had nestlings and fledglings ($P < 0.001$), then increased during the post-parental period ($P = 0.012$). Once nestlings were present, mass decreased more in females (9.7%) than in males (2.1%). The pattern of change in body mass with stage was different for the sexes (two-way ANOVA, $F_{5,1783} = 70.00$, $P < 0.001$) and correlates with the observation that more parental care was provided by females than males (Chapter 8).

Changes in the amount of fat visible through the skin, as quantified by fat class scores (Table 6.3), closely mirrored the changes in body mass (Fig. 6.3B). Males were quite lean throughout the reproductive period and often had no visible fat. Once they had stopped caring for fledglings their fat scores rose significantly (Kruskal-Wallis $H = 28.93$, $P < 0.001$). Females carried more fat than males in

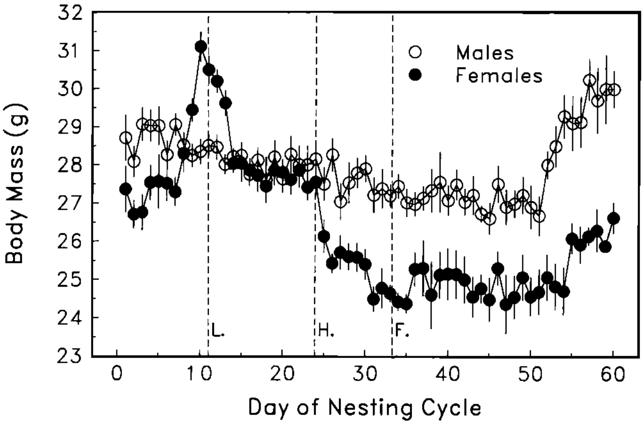

FIGURE 6.4. Mean body mass (± 1 SE) in *oriantha* by day of nesting cycle. Day 10 was day of first ovulation. Dashed line L shows when laying began, H when hatching began, and F when fledging occurred. Sample sizes 4–57 in females and 6–32 in males.

all six periods, particularly during the time before dependent young appeared (Fig. 6.3B), and the pattern of fat class with stage was different for the sexes (two-way ANOVA, $F_{5,1777} = 27.14$, $P < 0.001$). Females also exhibited considerable variation in their levels of fat between periods (Kruskal-Wallis $H = 227.19$, $P < 0.001$).

Daily Changes in Body Mass

Table 6.2 shows seasonal trends in body mass obtained from 18 different years. Body mass and fat class have been displayed in Fig. 6.3 according to the reproductive status of individuals known to be involved in breeding, but because they were compiled by calendar date or by various stages of involvement in reproduction, the data do not convey how body mass fluctuated day to day as the birds progressed through the nesting cycle. To see this, body mass data were normalized by using the day that females laid their first egg as a reference point. This was designated as being day 11 so the first ovulation was presumed to have occurred on the previous day, day 10. With the data thus set into synchrony, it can be seen that mass began to increase rapidly in females three days before their first ovulation (Fig. 6.4). Mean body mass on the morning of the first ovulation, 31.1 g, was the greatest measured on any one day of the nesting cycle. It then decreased slightly each morning thereafter until clutch completion, a reflection, no doubt, of a loss in ovarian mass as the largest follicles disappeared. Total mass loss during laying was about 3 g, or the equivalent of one egg. This shows that the resources required for a complete clutch were gathered both before and during laying, and that the patterns found in intraclutch egg mass variation (Chapter 7) could be either adaptive or constrained by nutrition, or combinations thereof (see Vinuela 1997).

During the 10 days following laying females were in full-time incubation, and they spent all night and 70–75% of the day on the nest, usually with their incubation patch applied to the eggs (Zerba and Morton 1983b). Based on calculations of heat exchange, Walsberg and King (1978) found that resting energy expenditure in an incubating *oriantha* at Hart Mountain, Oregon, was about 15% lower than expected for a bird perching outside the nest but exposed to the same microclimate.

Despite the advantage of being sheltered by the nest, body mass drifted down in females at Tioga Pass by about 0.5 g during the incubation period (Fig 6.4). This could have been due to resorption of the ovary and oviduct, but that should have occurred within the first few days after the onset of incubation (Ricklefs 1974). Furthermore, a sample of body weights taken from incubating females (1978 to 1981) showed that those with elevated nests were, on average, 5.1% lighter than those with ground nests (26.96 g, SD = 1.17 g, N = 20 vs. 28.40 g, SD = 1.39 g, N = 27; t = 3.77, $P < 0.001$). If changes in body mass of females reliably reflected changes in their energy balance, then it seems that it was more costly to incubate eggs in elevated sites where nests were exposed to convective cooling, than in those on the ground where they were tucked into more protected sites. Note, however, that fat scores were higher in females than in males even when their body mass was at its lowest (nestling and fledgling stages; Fig. 6.3)

Females began incubating before clutch completion, causing a hierarchy in embryo development and, eventually, asynchrony in hatching times. Hatching out of the total brood often took more than a day (Mead and Morton 1985) and the time frame for this process during the nesting cycle (Fig. 6.4) was from about day 24 to day 26. During this relatively brief period, body mass of females decreased by 8.0%, from a mean of 27.6 g to one of 25.4 g. Within the following few days mass decreased a bit more then stabilized at about 25 g for the next three weeks. Beginning at day 55, when fledglings were about 30 days of age, mass of females increased abruptly by about 6.5%. This gain may have been due to the release of females from parental duties because this was the age when young were known to achieve complete independence (Morton et al. 1972b).

Body mass of adult males decreased slowly but steadily from about 29 g to 27 g over a 50-d period (Fig. 6.4). Then, at day 52, they also showed an increase in mass, by about 8.5% over the next three days. As in females, this gain was likely related to cessation of parental care.

The pattern of body mass changes during the nesting cycle differed greatly in males and females except at the very end when both showed an increase. Before then females departed from males at two key times, once when they were synthesizing and laying eggs and again when hatching was taking place. That females should gain mass rapidly then lose it during production of the clutch whereas males, who do not produce eggs, remain at close to a steady state was no surprise. The large decrease in female mass that occurred during the hatching period seems less easy to explain, however. Why did females lose so much more than males during that two-day period and fail to gain it back? Observations of females at close range from blinds suggest that their mass loss was related to reduced food intake. While hatching was under way they usually sat very tightly, but also turned the eggs frequently, and sometimes stood up to assist an emerging chick by lifting off the eggshell and consuming it. They left for only brief intervals and returned with small bits of food for the chick(s). At some nests males began bringing food while hatching was still in progress and female behavior varied when this occurred. Sometimes they left the nest so the male could feed the young and sometimes they continued to brood, but took the food from the male and consumed it or passed it on to the hatchlings. Although activity at the nest was altered by these visitations, the usual degree of attentiveness associated with incubation (70% or more) was maintained during the hatching period (see Zerba and Morton 1983b, Table 3, incubation days 11 and 12). Attentiveness decreased immediately to about 50% once all chicks had hatched (Morton and Carey 1971). It seems that females lost mass during hatching because the time and energy devoted to foraging for hatchlings was subtracted from their own intake budget.

This tendency for females to be broody when hatching was still incomplete was carried to an extreme in nests wherein there was only one viable egg in the clutch. In these situations they spent so much time brooding unhatched eggs that the lone chick was stunted and did not survive.

A sudden decrease of mass in females, but not in males, when hatchlings begin to appear has been observed repeatedly in passerines (Freed 1981, Norberg 1981, Moreno et al. 1991, Woodburn and Perrins 1997), even when supplementary food was provided (Moreno 1991, Cavitt and Thompson 1997). Usually loss of mass in birds engaged in parental care has been attributed to energetic stress (Ricklefs and Hussell 1984), but some investigators have suggested that this is an adaptive, programmed response that has evolved because it reduces flight costs in the provisioning parents (Freed 1981, Norberg 1981, Jones 1994, Merkle and Barclay 1996). Freed (1981) discovered that female House Wrens lost about 13% of their body mass while feeding nestlings. Approximately half of the loss occurred before hatching was completed and the rest before food demands of the nestlings were greatest. Males provisioned at rates similar to those of females but showed no change in mass. Freed concluded that these patterns do not reflect stress (otherwise males would have lost mass too), and that the loss of mass in females saved them 23% in flight costs—a highly adaptive outcome. He does not explain why selection has favored acquisition of this supposed adaptation only in females, however. Not factored in either are the potential trade-offs or drawbacks of excessive weight loss to females. For example, desertion of clutches increased in Blue Tits (*Parus caeruleus*) when females were excessively lean (Merila and Wiggins 1997), so maintenance of good body condition would seem crucial to coping beyond the nesting phase with the high energy costs of feeding fledglings, with molting, and even to surviving (Slagsvold and Lifjeld 1989). Low body weights can also compromise a female's propensity to renest or double brood (De Laet and Dhondt 1989). Furthermore, field metabolism data indicate that maternal energy expenditure may not be tightly coupled to flight costs (Moreno et al. 1999).

The *oriantha* data are consistent with the hypothesis that mass loss occurs during parental care because it is energetically stressful; both sexes lost mass during the nesting cycle and gained it (and fat) immediately after their young became independent (Figs. 6.3, 6.4). Additional mass was lost in females at the time of hatching because incubation-levels of attentiveness were maintained and decreased self-maintenance (voluntary starvation) occurred as they attempted to facilitate hatching of all eggs in the clutch and, possibly, to minimize hatching asynchrony. The latter points to ultimate causation, to the reason that this response evolved in the first place. In addition, these brooding propensities probably caused differential growth rates early in nestling life that were dependent upon hatching order (see Chapter 8 for more discussion).