

## Effects of weather on daily body mass regulation in wintering dunlin

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### Summary

We investigated the influence of changes in weather associated with winter storms on mass balance, activity and food consumption in captive dunlin (*Calidris alpina*) held in outdoor aviaries, and compared the aviary results with weather-related body mass differences in free-living dunlin collected at Bolinas Lagoon, California. Captive birds fed *ad libitum* increased their body mass at higher wind speeds and lower temperatures, suggesting regulation of energy stores, whereas free-living birds exhibited patterns suggesting thermoregulatory limits on body mass regulation. Daily energy expenditure in aviary dunlin was 2.85 kJ g d<sup>-1</sup>, or 2.8× basal metabolic rate (BMR), with thermostatic costs averaging 59% of daily expenditure. Slight but significant increases in body mass and energy expenditure in captive birds on rainy days, adjusted for possible external water mass, suggested

rainfall as a proximate cue in regulating daily body mass. Body mass changes under artificial rainfall indicated similar results, and field masses suggested that free-living birds have greater body mass on days with measurable rainfall. Increased activity costs under artificial rainfall were associated with an increase in maintenance activities, relative to controls. Whether activity costs increased on days with natural rates of rainfall was unclear. Our results are consistent with current hypotheses regarding the role of body mass regulation in providing insurance against increased starvation risk during deteriorating thermal or foraging conditions, or in reducing the costs of extra mass as conditions improve.

Key words: *Calidris alpina*, dunlin, shorebird, wader, energy balance, rainfall, winter storm, Tomales Bay, Bolinas Lagoon.

### Introduction

Storing reserve energy in body tissues during winter improves fasting endurance (King, 1972; Blem, 1976, 1990), and enhances the ability of some species to move to more profitable areas when feeding conditions deteriorate (Evans, 1976; Warnock et al., 1995). By accumulating internal energy stores in anticipation of such needs, birds avoid using energy in body structures needed for normal function, but mobilising it in emergencies to avoid starvation (van der Meer and Piersma, 1994). However, increasing energy stores carries additional costs. It requires additional foraging time, which may increase exposure to predators, and increases wing loading and inertia, which may reduce a bird's ability to avoid predators by compromising its agility (Lima, 1986; Witter and Cuthill, 1993). Theoretical work suggests that birds should minimize winter mortality by regulating body mass associated with energy stores in a manner that balances risks of predation and starvation (Lima, 1986; McNamara and Houston, 1990; Houston and McNamara, 1993). Body mass should also vary with perceived risk of starvation, based on changing thermal or foraging conditions. Indicators of winter storms in temperate estuaries are likely to predict such changes, not only because winter storms increase thermal stress, but because the

abundance and availability of invertebrate prey are inversely associated with storm-related rainfall and runoff (Page and Stenzel, 1975; Goss-Custard, 1984; Nordby and Zedler, 1991).

An important question in understanding the evolution of body mass regulation is over what time periods birds must balance energy intake and expenditure to maximize fitness. Many studies of body mass variation have focused on seasonal or intraseasonal patterns relative to demands such as migration and reproduction (Holmes, 1966; King, 1972; Blem, 1976; Pienkowski et al., 1979; Nolan and Ketterson, 1983; Biebach, 1996). As opportunities to replenish daily energy stores decline in winter, birds may improve their chance of survival by increasing daily minimum mass to gradually achieve winter fattening (Lehikoinen, 1987), or conversely, by reducing energy storage as conditions improve. There is general agreement that photoperiod, being closely associated with long-term temperature, is the most likely proximal cue underlying seasonal regulation of energy stores (Blem, 1990; Biebach, 1996). Winter body mass patterns in grey plover *Pluvialis squatarola* (Dugan et al., 1981), dunlin *Calidris alpina* (Pienkowski et al., 1979) and red knot *Calidris canutus* (Piersma et al., 1995) are similar among years, suggesting that

internal programming based on long-term average conditions is important. However, the short-term and episodic variability of thermal or foraging conditions that characterize temperate winters seems to challenge the adaptive value of energy stores based on long-term averages.

Several authors have investigated, with varying success, the coupling of seasonal energy storage with climatic conditions over shorter periods. Dawson and Marsh (1986) found that fat content in American goldfinch *Carduelis tristis* was not correlated with temperature over any time scale, and concluded that winter fat stores were independent of short-term variations in ambient temperature and are instead determined by long-term variables. In contrast, Zwarts et al. (1996) found that correlations indicating body mass decline in oystercatcher *Haematopus ostralegus* under harsh environmental conditions, primarily increased wind speed, were strongest on the day of capture. In a study of latitudinal variation in white-crowned sparrows *Zonotrichia leucophrys gambelii*, King and Mewaldt (1981) argued that winter fat stores are maintained at maximal quantities as an adaptation to unpredictable episodic environmental stresses. The most adaptive way to maintain energy stores may be to fine-tune seasonal patterns of storage based on long-term average requirements, with short-term regulation based on selection for tissue deposition, to increase energy stores during harsh weather, and counterselection for light mass and predator avoidance during milder periods (Blem and Shelor, 1986).

Evidence that reductions in air temperature stimulate daily increases in body mass has been found in some species (Nolan and Ketterson, 1983; Ekman and Hake, 1990; Gosler, 1996; Lilliendahl et al., 1996), but not in others (King, 1972; Dawson and Marsh, 1986). Mascher (1966) found a tendency toward mass loss in dunlin associated with lower daily temperature, while December masses of dunlin among various wintering sites in Britain were inversely related to mean December temperatures (Pienkowski et al., 1979). In general, field studies of shorebirds (Charadriiformes) suggest that wind reduces body mass during winter storms, with mass loss correlating more closely with wind speed than with temperature (Davidson, 1981; Dugan et al., 1981; Zwarts et al., 1996).

Current evidence suggests that body mass in shorebirds declines gradually throughout winter, except during periods of severe thermal or foraging stress when energy balance cannot be maintained (Dugan et al., 1981; Pienkowski et al., 1984). This scenario suggests a compensatory strategy to stabilize energy stores at levels adequate for surviving severe events. However, when thermal or foraging conditions are highly variable and extreme events are likely, it may be more effective to over- or undercompensate slightly for anticipated changes in starvation risk. For example, a bird anticipating a winter storm might accept a slight increase in predation risk or other costs associated with extra mass as a hedge against the increasing likelihood of extreme food scarcity (Boyce, 1986; Biebach, 1996).

Shorebirds store energy as both fat and lean mass, which are apparently deposited and used at constant rates (Davidson,

1984; van der Meer and Piersma, 1994; Lindström et al., 2000). Depletion of energy stores is marked by an increase in protein catabolism, which presumably signals the loss of structural reserve tissue (van der Meer and Piersma, 1994). Dunlin wintering in Britain maintain greater lean mass (mostly pectoral muscle) in estuaries with lower average winter air temperatures, suggesting that lean winter body mass, as well as fat mass, is adjusted to local climate (Davidson et al., 1986).

The behavioral responses of shorebirds to winter storms are known to include movements to sheltered or more profitable feeding areas (Evans, 1976; Connors et al., 1981; Warnock et al., 1995; Kelly, 2001), but whether responses to short-term changes in weather might involve regulation of internal energy stores is not clear (Zwarts et al., 1996). Small shorebirds in temperate latitudes generally store only 1.5–4 days of reserve energy (Castro et al., 1992; Piersma et al., 1994), although inclement winter weather often persists for periods that long or longer. Therefore, regulation of energy stores should reflect the risks of thermal or foraging conditions deteriorating beyond the fasting capacity of individuals.

In this study, we investigated the extent to which changes in daily energy balance in dunlin reflect conditions associated with the arrival and departure of winter storms. We tested the influences of weather on daily changes in body mass, energy intake and, based on mass balance, activity costs in captive dunlin. We compared the results with body mass differences in free-living dunlin, based on field masses collected over 14 years. Because rainfall strongly influenced dunlin body mass in captivity and in the field, we also examined the discrete effects of rainfall as a possible proximate cue used to regulate body mass, and conducted an experiment using artificial rainfall. Our results provide evidence that body mass regulation in winter occurs in response to daily changes in weather.

### Materials and methods

Unless birds are starving, changes in body mass result from using energy contained in storage depots rather than that contained in structural tissues necessary for normal life (van der Meer and Piersma, 1994). Therefore, we used change in body mass of dunlin fed *ad libitum* as an index of daily changes in stored energy and expressed the data as proportional change in body mass to control for differences in the sizes of individuals. We used stepwise linear regression to test for influences of weather on daily changes in body mass, energy intake and activity costs. We then used general linear models with significant predictors from the stepwise regressions as covariates to test for discrete effects of rainfall on changes in body mass. We used repeated measures in all analyses to account for random variation among individual birds sampled; when individual variation was not significant ( $P=0.28\text{--}0.98$ ), within-subjects responses were generally pooled with error variation.

#### Captive birds

We captured dunlin in mist nets during November and

December of 1997 ( $N=15$ ) and 1998 ( $N=16$ ), on the tidal deltas of Walker and Lagunitas creeks in Tomales Bay, California. Birds were held under natural weather conditions in outdoor aviaries midway along the east shore of Tomales Bay, and released prior to spring migration. We separated individuals into two groups housed in adjacent aviaries 5.5 m × 6 m × 2.5 m high. Each aviary had a sand floor and a shallow wading pool along one side, and was approved by University of California Protocol for Animal Use and Care (No. 7481). Except during periods of imposed fasting, dunlin were fed *ad libitum* on Aquamax Fry Starter (5D00, Purina Mills, Inc., St Louis, MO, USA). Dunlin were allowed to adjust to captivity for at least 3 weeks, and prior to data collection they maintained stable body mass slightly above capture mass. Body mass in each bird was measured daily, approximately 1 h after dark, using a digital balance calibrated to an accuracy of 0.01 g.

#### Weather

We used a Campbell Scientific 21X microdata logger to record weather conditions inside the aviary. Ambient and operative temperature, wind speed and solar radiation data were recorded at 60 s intervals and averaged every 0.5 h. Wind speed was measured with a Thornthwaite model 901-LED sensitive cup anemometer near ground level (dunlin height). Ambient air temperature was measured with a shaded copper–constantan thermocouple mounted near the ground. Solar radiation was monitored with a factory-calibrated LICOR model 200 pyranometer at ground level. We obtained barometric pressure data from the University of California Bodega Marine Laboratory, approximately 25 km northwest of the study site. Rainfall was measured twice daily on site using a manual rain gauge. We used four unheated copper dunlin mounts, faced in different directions, to estimate operative temperature (Bakken and Gates, 1975; Bakken, 1976). We calculated standard operative temperature by adjusting for the effects of wind speed using the procedure presented by Bakken (1990), which is based on a general relationship between wind effects and thermal conductance in ten passerine and seven non-passerine species. Estimates may include some inaccuracies associated with complex effects of environmental conditions on the use of taxidermic mounts (Walsberg and Wolf, 1996). Because the taxidermic mounts would be damaged by rainfall, we estimated operative temperature on days with rainfall using a metal sphere thermometer (9 cm diameter) painted flat gray, recalibrated with data from the copper dunlin mounts (Walsberg and Weathers, 1986); metal sphere temperatures were closely related to those measured by the copper mounts ( $r^2 > 0.98$ ). To analyze weather effects on field masses collected in Bolinas Lagoon, we used daily weather data from the Palomarin Field Station of the Point Reyes Bird Observatory, approximately 3.2 km west of the field site.

#### Daily body mass

To examine intraseasonal trend in body mass, we used Cleveland's locally weighted regression algorithm (LOWESS)

(Cleveland, 1979; Chambers et al., 1983). This method uses locally weighted least-squares and a robust fitting procedure to define smoothed points that are relatively insensitive to outlying values, and allows a flexible degree of smoothing by adjusting the proportion of data scanned ( $f$ ) for each fitted value. We then estimated the intraseasonal trend before and after the point of maximum body mass, using repeated-measures regression to account for differences among individuals.

To test feeding and body mass responses to natural weather patterns, we regressed food consumption and proportional body mass change against daily weather variables. We measured average daily food consumption within each test group as the difference between the constant dry-mass equivalent of food supplied and constant dry-mass of food removed each day. Candidate independent weather variables used in stepwise modeling were: average and maximum wind speed ( $\text{m s}^{-1}$ ); barometric slope ( $10^2 \text{ Pa h}^{-1}$ ) during 12, 18 and 24 h prior to daily body mass measurements; diurnal rainfall (cm) during 10 h immediately prior to daily body mass measurement; nocturnal rainfall (cm) during 14 h immediately prior to the previous diurnal period; diurnal and nocturnal rainfall (cm) on each of 3 days prior to body mass measurement; minimum, average and maximum daily air temperature ( $^{\circ}\text{C}$ ); and minimum, average and maximum solar radiation ( $\text{W m}^{-2}$ ). We also included daily change in each of these variables as candidate predictors.

Independent variables were allowed to enter the regression models only if product–moment correlations were less than 0.30. When pairs of variables exceeded this level, the variable with the lowest  $F$ -value was omitted. Residuals of proportional body mass change did not differ significantly from normality, and variances were stable. Residuals showed no significant evidence of autocorrelation ( $|r| < 0.15$ ,  $P > 0.05$ , power  $> 0.90$ ), so sequential daily measurements were considered to be independent.

To examine discrete effects of rainstorms on body mass regulation, we developed general linear models of daily body mass change in birds fed *ad libitum* on days with and without rainfall, including significant predictors from the stepwise regressions as covariates. In corroborative tests, we compared simultaneous body mass responses of dunlin fed *ad libitum* with and without artificial rainfall. The water used for artificial rain was pumped from a shallow reservoir near the aviaries and was similar in temperature to average ambient air temperature. Test groups of 8 and 9 individuals were housed in adjacent aviaries and 'rainfall' treatment alternated between groups and aviaries over four trials separated by at least 2 weeks. During each trial, 'rainfall' sprinklers were turned on for 10 h immediately preceding the normal evening weighing time (approximately 1 h after dark). Results were adjusted for external water mass in the 'rainfall' group (see below). All tests using artificial rainfall were conducted on days with complete cloud cover and no natural precipitation.

#### External water mass

To account for possible external water mass retained in

plumage on rainy days, and to adjust for this possibility in measurements of body mass, we measured the amount of external water mass in eight captive dunlin subjected to artificial rainfall. Before each of two trials, birds were separated into two groups (experimental and control) of four individuals each in separate outdoor aviaries, and allowed to adjust to the separation with *ad libitum* food and water for 2 days. On the third day, food was removed from both groups for 4 h, each individual was weighed, and then sprinklers mounted 1 m above one of the aviaries were turned on to simulate rainfall for 8 h (trial 1) and 18 h (trial 2). Control and 'rainfall' groups continued fasting during this treatment phase. Immediately after each treatment period, we placed each group of birds into a well-ventilated plastic box in a darkened room maintained at 24 °C and 43 % relative humidity. The boxes were identical (0.45 m × 0.30 m × 0.40 m high), with all sides reduced to bars and openings to allow for unimpeded air flow. We immediately weighed each individual in both groups, beginning with the 'rainfall' group, and repeated the process every 15 min for 3.5 h. After the last weighing interval, all birds were returned to the aviaries with *ad libitum* food and water for 2 days before the second trial. On the second trial, control and 'rainfall' groups were reversed.

We used repeated-measures quadratic regression to model rates of post-treatment mass loss in 'rainfall' and control groups. The 'rainfall' group was considered to be dry when instantaneous rates of mass loss were equal between groups. We estimated mass attributable to external moisture as the difference in post-treatment mass loss between groups when both groups of fasting birds were dry.

The artificial rainfall occurred at a relatively heavy rate of  $4.04 \pm 0.40 \text{ cm h}^{-1}$  (mean  $\pm$  S.E.M.,  $N=30$  measurements evenly distributed within the aviary). This rate far exceeded rates of natural rainfall ( $\bar{x}=0.08 \pm 0.016 \text{ cm h}^{-1}$ , mean  $\pm$  S.E.M., max.=0.31,  $N=33$  days). Therefore, adjustment for possible external water mass based on these results may be too large, or should be considered as the maximum amount of additional mass that is likely to occur. Rainfall did not generally occur during banding sessions when field masses were measured, even when measurable rainfall was recorded for those days, so any water that might be trapped in feathers probably had time to dry. Alternatively, if birds became wet during banding, because of extended handling or temporary captivity, external water mass might have substantially influenced the field mass. Finally, some or all of any added water mass might be compensated for by unmeasured capture-related weight loss (Davidson, 1984; Warnock et al., 1997). To account for the possibility of external water mass on days with rainfall, we adjusted body mass data in all analyses according to estimates of external water mass under heavy artificial rainfall, and compared models using adjusted and unadjusted values.

#### Activity costs

We quantified activity budgets of captive dunlin in control and artificial-rainfall groups, from a concealed position in a blind near the aviary. Frequencies for each activity were

recorded during continuous, 10 min observations of focal individuals (Altmann, 1974). Observations were conducted on fasting birds during the test for external water mass described above, therefore the observed activities did not include feeding or foraging behaviors. To improve the independence of observations, focal periods were at least 10 min apart ( $N=33$ ).

By deduction, activity costs ( $\text{kJ g d}^{-1}$ ) of fasting birds under artificial rainfall could be represented by the equation:

$$\text{Activity cost} = \text{UE} \times \text{RE}[1-(M_t/M_{t-1})] - \text{TR} - \text{BMR}. \quad (1)$$

Assuming that utilization efficiency (UE), density of energy stored in reserve body mass (RE) in  $\text{kJ g}^{-1}$ , thermoregulatory cost (TR) in  $\text{kJ g d}^{-1}$ , and basal metabolic rate (BMR) in  $\text{kJ g d}^{-1}$ , did not differ between simultaneous treatment and control groups of fasting birds, daily differences in proportional body mass loss  $[1-(M_t/M_{t-1})]$  should be proportional to differences in activity costs. Thus, if UE below maintenance is 0.92 (Blaxter, 1989), the difference in activity cost between fasting groups would be 92 % of the difference in energy value of body mass loss, in  $\text{kJ g d}^{-1}$ . This model assumes that activity costs in dunlin are additive. If heat produced as a by-product of activity partially substitutes for thermoregulatory costs (Webster and Weathers, 1990; Bruinzeel and Piersma, 1998), then our modeled activity costs would represent only unsubstituted costs. Poot and Piersma (1994) suggested that heat substitution in exercising red knots *Calidris canutus* was cancelled out by increased thermal conductance (Bruinzeel and Piersma, 1998). Based on this, they calculated the added costs of activities as the residual of average daily metabolic rate minus maintenance. The temperature of artificial rainfall was similar to ambient air temperature, but we did not measure the possible effect of artificial rainfall on operative temperatures experienced by the birds. Birds felt dry to the touch immediately after treatment, suggesting that the thermal properties of the plumage were not degraded. If feathers did not get wet or matted and the layer of air held by feathers was not reduced, exterior moisture should have had little if any effect on insulation (Kennedy, 1970; Kendeigh et al., 1977; Lustick and Adams, 1977; Stalmaster and Gessaman, 1984). Therefore, a body mass decline in the 'rainfall' group relative to controls (when both groups were dry) reflected the cost of activities, or alternatively the unsubstituted cost of activities, associated with rainfall, independent of the cost of foraging (since birds were fasting).

To examine the influence of natural weather patterns on daily activity costs in fed birds, we derived estimates of activity energy expenditure, in  $\text{kJ g d}^{-1}$ , from this equation:

$$\begin{aligned} \text{Activity cost} = \\ (1-\text{HI})\text{AE} \times \text{GEI} - \text{RE}[(M_t/M_{t-1})-1] - \text{TR} - \text{BMR}, \quad (2) \end{aligned}$$

where HI is heat increment of feeding, AE is assimilation efficiency (digestible proportion of gross energy intake), GEI is gross energy intake in  $\text{kJ g d}^{-1}$  and  $[(M_t/M_{t-1})-1]$  is the proportional change in body mass (adjusted for possible external water mass). The energy costs of biosynthesis and catabolism of stored tissue are components of HI (Blaxter,



1989). As in Equation 1, this model assumes that activity costs are additive, or alternatively that estimated activity costs represent only the unsubstituted portion of activity. In addition, the model assumes that HI does not substitute for TR. The extent to which substitution might occur is controversial (Dawson and O'Connor, 1996). Therefore, we considered the possible effects of substitution by evaluating the results with and without HI. We initially assumed a gross utilization efficiency  $(1-HI)AE$  of 0.64, based on an assimilation efficiency of 0.80 and utilization efficiency of metabolizable energy  $(1-HI)$  of 0.80 (Ricklefs, 1974; Blaxter, 1989; Castro et al., 1989; Klaassen et al., 1990). The proportion of fat represented in dunlin energy stores, based on regressions of lean and fat mass on body size and total body mass, was estimated at 50–67% prior to spring migration in northwest Africa (Piersma and van Brederode, 1990). Therefore, we initially assumed an energy density of retained body tissue (RE) of  $23.61 \text{ kJ g}^{-1}$  wet mass (55% fat; lean mass: 68.3% water, 26.7% protein, 5% ash) (Piersma and van Brederode, 1990). The sensitivity of the results were tested across the range of possible values for gross utilization efficiency and RE. We determined TR and BMR using standard operative temperatures measured in the aviary (see above) and corresponding measurements of resting metabolic rates for dunlin wintering on Tomales Bay (Kelly, 2000). We calculated GEI by multiplying the dry mass of food ingested by the energy density of the food ( $23.95 \text{ kJ g}^{-1}$  dry mass; Mark Griffin, Purina Mills, Inc., personal communication).

#### Field mass

We examined body mass regulation in free-living dunlin by testing differences in mass of dunlin banded from 1979 to 1992 at Bolinas Lagoon, California, an estuary approximately 20 km south of Tomales Bay. To adjust for capture-related loss of body mass (mostly water) (Davidson, 1984), we estimated body mass declines from the data plotted for 212 individuals measured twice but not immediately after capture. To estimate capture-related loss of body mass, we used the integral of the power function relating the linear slope of mass loss between sequential measurements to the midpoint of time (min) since capture:

$$\text{Proportional body mass loss} = 0.0046[\text{time since capture}]^{0.573}. \quad (3)$$

We derived alternative parameter estimates from intensive repeated measures of body mass in 43 dunlin captured at Tomales Bay, 22 km north of Bolinas Lagoon. A calibrated digital balance was used to measure individuals to the nearest 0.02 g immediately upon removal from mist nets 0–10 min after capture and 1–5 additional occasions over periods of up to 4 h. The resulting parameter estimates did not differ significantly from those derived from banding masses at Bolinas Lagoon ( $t$ -tests,  $P > 0.60$ ). We used Equation 3 to correct body mass values in 367 dunlin weighed in the field at Bolinas Lagoon with time known since capture.

Stepwise linear regression was used to identify weather

variables that significantly predicted differences in body mass among free-living dunlin (corrected for time since capture), with days since 1 October and exposed culmen length as covariates to control for intraseasonal trend and body size. Field masses did not differ significantly between years relative to within-year variation ( $F_{11,63}=1.9$ ,  $P > 0.44$ ), so we assumed that dunlin responded to weather in a consistent manner across the years. We then developed general linear models, including significant predictors identified in the stepwise regressions, to test for discrete effects of rainstorms on body mass change. We compared the results with identical analyses based on the entire sample of field masses ( $N=995$ ), which were not adjusted for capture-related weight loss.

#### Results

Body mass of captive dunlin did not differ significantly between juveniles and adults ( $F_{1,29}=0.23$ ,  $P=0.63$ ) or between years ( $F_{1,29}=0.07$ ,  $P=0.79$ ). Individual body mass of captive dunlin increased at a rate of  $0.233 \pm 0.019 \text{ g d}^{-1}$  (mean  $\pm$  S.E.M.) from 16 to 28 December and declined on average by  $0.063 \pm 0.003 \text{ g d}^{-1}$  (mean  $\pm$  S.E.M.) from 28 December to 12 March (Fig. 1). The slope of this decline did not differ significantly between years ( $t_{27}=0.52$ ,  $P=0.61$ ) or between juveniles ( $N=20$ ) and adults ( $N=11$ ;  $t_{27}=0.28$ ,  $P=0.79$ ). Field masses from Bolinas Lagoon, independent of age, bill size and capture-related weight loss ( $N=358$ ), declined by  $0.032 \text{ g d}^{-1}$  from 21 October to 27 January ( $N=358$ ); masses uncorrected for capture-related mass loss declined  $0.029 \text{ g d}^{-1}$  from 19 October to 5 March ( $N=999$ ). Neither regression of field data showed a midwinter peak as suggested by trends for captive birds.

#### Artificial rainfall

Birds generally felt dry to the touch even after treatment with artificial rainfall. Occasionally we detected small amounts of external moisture on birds during the weighing process.

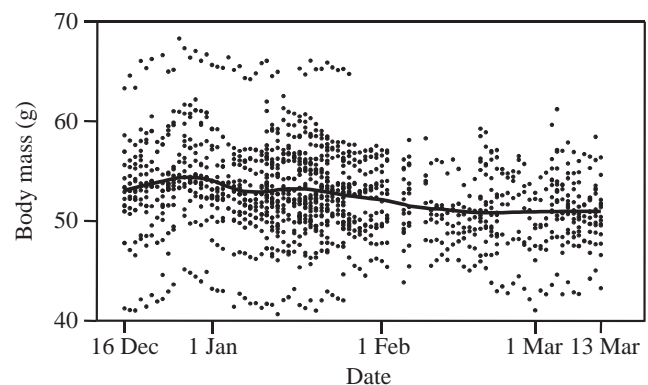


Fig. 1. Scatterplot of intraseasonal body mass change in captive dunlin at Tomales Bay, California, 1997–8 and 1998–9. The trend line was estimated using LOWESS, a locally weighted regression algorithm (Cleveland, 1979); smoothing parameter,  $F=0.25$  of data scanned for each fitted value.

Quadratic models closely fit the overall patterns of mass loss during drying periods for both control and 'rainfall' groups ( $r^2 > 0.99$ ; Fig. 2, top). The plumage of birds subjected to artificial rainfall was dry after 163 min, when instantaneous rates of mass loss were equal between control and 'rainfall' groups. At this point, post-treatment mass loss associated with loss of external water mass was  $0.0079 \pm 0.001 \times \text{body mass}$  (mean  $\pm$  S.E.M.,  $N=160$ ). Similarly, non-significant differences in linear rates of mass loss suggested that plumage was dry after 100 min ( $P > 0.05$ ) and that external water mass associated with artificial rainfall was  $0.0075 \pm 0.0003 \times \text{body mass}$  (mean  $\pm$  S.E.M.,  $N=80$ ). We therefore adjusted body mass changes on days with real or artificial rainfall by subtracting 0.008 from the measured proportions. Based on this difference, rain water trapped in plumage during heavy artificial rainfall increased

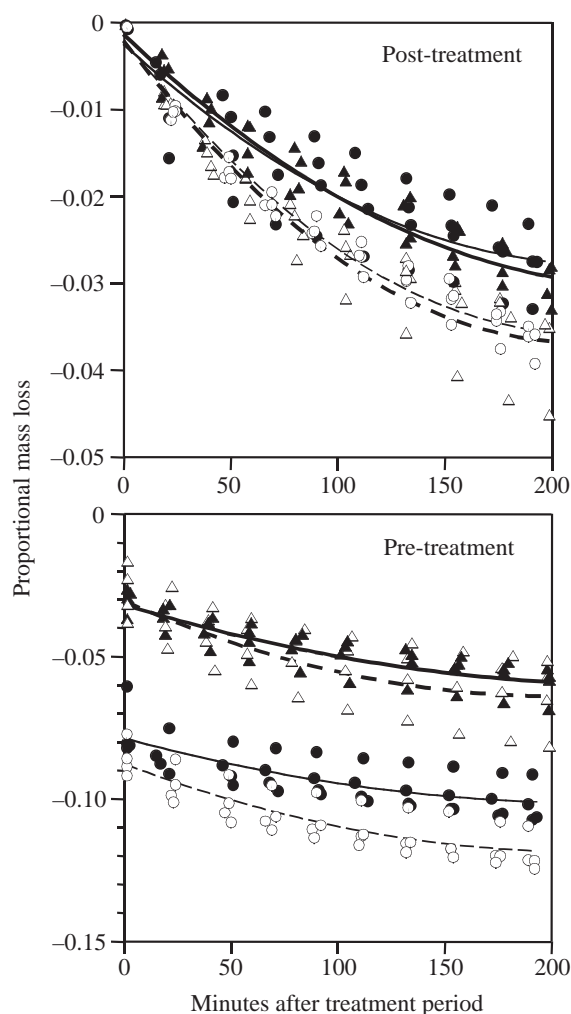


Fig. 2. Quadratic trends in mass loss of fasting dunlin allowed to dry after periods of artificial rainfall, indicating water retention in plumage (top) and accelerated body mass loss (bottom). Open symbols and broken lines represent 'rainfall' birds; solid symbols and solid lines represent control birds. Triangles and bold lines represent responses to 8 h of artificial rainfall; circles and thin lines represent responses to 18 h of artificial rainfall.  $r^2 > 0.99$ .

body mass measurements by approximately 0.4 g in a 50 g dunlin.

After allowing moisture in plumage to dry, body mass loss in fasting dunlin under artificial rainfall was significantly greater than in controls ( $F_{1,12}=6.1$ ,  $P=0.03$ ; Fig. 2, bottom), independent of trial ( $F_{1,12}=2.3$ ,  $P=0.16$ ). When analyzed separately, the second trial revealed significant rain-related mass loss ( $F_{1,6}=12.5$ ,  $P=0.01$ ), but differences in the first trial, based on only four treatment individuals, were not great enough to indicate significance ( $P > 0.05$ ). Activity costs in fasting birds were also greater under artificial rainfall, assuming that changes in activity costs while fasting were proportional to body mass loss (see Materials and methods). These increases in activity were consistent with results from dunlin fed *ad libitum* under natural rainfall (see below).

Dunlin fed *ad libitum* under artificial rainfall significantly increased their body mass by a factor of  $0.015 \pm 0.0038$  (mean  $\pm$  S.E.M.) compared to  $0.004 \pm 0.0036$  (mean  $\pm$  S.E.M.) in controls, based on masses adjusted for possible water retention in plumage ( $F_{1,64}=4.27$ ,  $P < 0.05$ ). This difference represented an increase of 0.55 g in a 50 g dunlin. Although these results were statistically significant, they should be considered preliminary because they were based on only 4 days of observation (trials) during which other interacting environmental conditions (barometric pressure, temperature, wind) might have had an effect. In addition, the differences were not great enough to indicate significance when trials were analyzed separately, based on eight birds per group.

Behavioral observations suggested that the costs of maintenance activities were greater under artificial rainfall (Table 1). In particular, a greater frequency of behaviors that keep rain from penetrating the plumage, such as head, wing and body shakes, and more walking/running, characterized activity associated with rainfall. Tail shakes did not differ significantly between groups, possibly because of minimal thermal protection provided by rectrices, but body shakes functioned to remove water from tail, wings, back and head.

Table 1. Activities of captive dunlin under artificial rainfall and of control birds

Activity	'Rainfall' group	Control group	P
Walking or running (steps)	$4.64 \pm 0.35$	$2.73 \pm 0.35$	$< 0.001$
Body shake	$1.04 \pm 0.26$	$-0.77 \pm 0.25$	$< 0.0001$
Head shake	$1.99 \pm 0.20$	$-1.75 \pm 0.20$	$< 0.0001$
Wing flap	$-0.83 \pm 0.26$	$-1.93 \pm 0.25$	$< 0.01$
Tail shake	$-0.23 \pm 0.32$	$-0.86 \pm 0.31$	0.16
Head scratch	$-1.10 \pm 0.36$	$-1.51 \pm 0.36$	0.43
Preen (seconds)	$-0.27 \pm 0.55$	$-0.17 \pm 0.53$	0.89
Fly-up	$-1.96 \pm 0.31$	$-1.78 \pm 0.31$	0.68

Values are based on frequencies within 10-minute focal observations and are means  $\pm$  S.E.M. ( $N=16$  for rainfall group;  $N=17$  for control group).

Data are transformed as  $y = \ln(\text{activity} + 0.1)$ .

Table 2. Stepwise multiple regression of proportional body mass change in captive dunlin (dependent variable, N=902) on daily weather variables

Independent variable	Coefficient $\pm$ S.E.M.	Standard coefficient	F	P
Change in diurnal rainfall (cm)				
Adjusted	0.005 $\pm$ 0.0008	0.19	30.34	<0.0001
Unadjusted	0.006 $\pm$ 0.0008	0.24	52.77	<0.0001
Change in minimum temperature ( $^{\circ}$ C)				
Adjusted	-0.001 $\pm$ 0.0002	-0.19	25.49	<0.0001
Unadjusted	-0.001 $\pm$ 0.0002	-0.21	33.12	<0.0001
Minimum wind speed ( $\text{m s}^{-1}$ )				
Adjusted	0.157 $\pm$ 0.042	0.13	14.13	<0.0001
Unadjusted	0.132 $\pm$ 0.042	0.11	9.81	0.002
Solar radiation ( $\text{kW m}^{-2}$ )				
Adjusted	-0.036 $\pm$ 0.011	-0.13	11.76	<0.0001
Unadjusted	-0.053 $\pm$ 0.011	-0.18	25.11	<0.0001
Barometric slope ( $10^2 \text{ Pa h}^{-1}$ )				
Adjusted	0.136 $\pm$ 0.074	0.07	3.39	0.07
Unadjusted	0.153 $\pm$ 0.075	0.08	4.20	0.04

The predictor variables entered for models based on body mass adjusted for possible rain water retention in plumage ( $r^2=0.16$ ) and those based on unadjusted body mass ( $r^2=0.22$ ) were the same.

#### Daily body mass and activity costs in captivity

Stepwise regressions identified four weather variables as highly significant but weak predictors of proportional body mass change (Table 2). Body mass increased significantly with increasing rainfall, increasing minimum wind speed, decreasing maximum daily air temperature, and decreasing solar radiation. Bivariate plots showed no evidence of nonlinear thresholds. Coefficients (slopes) of weather effects did not differ significantly between juveniles and adults or between years ( $t$ -tests,  $P>0.05$ ). Analyzing days with and without rainfall (cm) separately had no effect on the sign or significance of the coefficients for temperature ( $^{\circ}$ C), wind ( $\text{m s}^{-1}$ ) or solar radiation ( $\text{kW m}^{-2}$ ). Based on adjusted values, daily proportional change in body mass =  $-0.025 + 0.005$  change in diurnal rainfall  $- 0.001 \times$  change in minimum temperature  $+ 0.157 \times$  minimum wind speed  $- 0.036 \times$  solar radiation  $+ 0.136 \times$  barometric slope ( $10^2 \text{ Pa h}^{-1}$ ). Daily fluctuations in body mass were greater in 1997–98 than in 1998–99 ( $F_{539,531}=1.18$ ,  $P<0.05$ ), reflecting greater variation in rainfall, average temperature, and wind speed in 1997–98 ( $P<0.001$ ). After accounting for weather effects, daily variation did not differ between years ( $P>0.05$ ).

Dunlin body mass increased significantly at a proportional rate of  $0.006 \text{ d}^{-1}$  on days with rain (adjusted for possible external water mass) relative to days without rain ( $F_{1,962}=9.14$ ,  $P<0.01$ ). This difference was based on consistent proportional body mass decline on days without rainfall of  $0.005 \text{ d}^{-1}$  ( $t_{812}=5.34$ ,  $P<0.001$ ) and a small, non-significant proportional increase of  $0.001 \text{ d}^{-1}$  on rainy days ( $t_{187}=0.82$ ,  $P=0.41$ ). Unadjusted values increased significantly by  $0.014 \text{ d}^{-1}$  on rainy days relative to days without rain ( $F_{1,962}=51.63$ ,  $P<0.001$ ).

Daily food intake, based on average group consumption ( $N=80$ ), increased significantly with greater rainfall during the 10h period prior to daily body mass measurement ( $F_{1,76}=15.18$ ,  $P<0.001$ ). No other weather variables entered the stepwise regression. By excluding rainfall as a predictor, an alternative model revealed significantly greater food consumption on days with lower or more negative barometric slope ( $F_{1,61}=6.95$ ,  $P=0.01$ ), greater average wind speed ( $F_{1,61}=6.81$ ,  $P=0.01$ ) and, marginally, dropping temperatures ( $F_{1,61}=3.62$ ,  $P=0.06$ ). On average, dunlin consumed  $0.030 \pm 0.008 \text{ g (g d)}^{-1}$  (mean  $\pm$  S.E.M.) more food on days with rain than on days without rain ( $F_{1,76}=14.78$ ,  $P<0.001$ ). This was equal to an average increase in gross energy intake of  $0.64 \pm 0.019 \text{ kJ g d}^{-1}$  (mean  $\pm$  S.E.M.) on days with rainfall.

Based on initial estimates of gross utilization efficiency (0.64) and energy density of stored body tissue ( $23.61 \text{ kJ g}^{-1}$ ), stepwise regression suggested that activity costs, adjusted for possible external water mass, increased significantly with: (1) greater rainfall during 10h before daily body mass measurements ( $F_{1,466}=26.50$ ,  $P<0.001$ ); (2) higher average air temperature ( $F_{1,466}=20.63$ ,  $P<0.001$ ); and (3) lower or more negative barometric slope during the previous 12h ( $F_{1,466}=20.59$ ,  $P<0.001$ ). Activity costs were significantly greater on days with rain ( $1.42 \pm 0.037 \text{ kJ g d}^{-1}$ , mean  $\pm$  S.E.M.) than on days without rain ( $1.11 \pm 0.029 \text{ kJ g d}^{-1}$ , mean  $\pm$  S.E.M.;  $F_{1,525}=38.14$ ,  $P<0.0001$ ). This difference is illustrated in the sensitivity analysis (Fig. 3), which further indicates that the significance of rain-related increases in activity costs was insensitive to variability in likely values of gross utilization efficiency and energy density (fat content) of tissue stores. If HI substitutes for TR, then some or all of the heat produced in

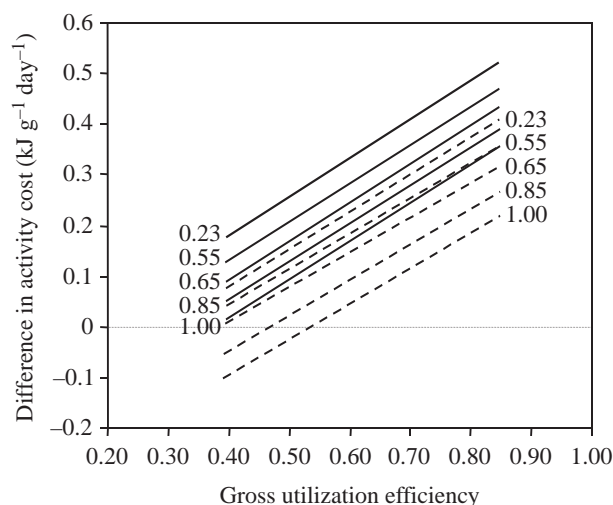


Fig. 3. Sensitivity analysis of rainfall-related increases in activity costs, adjusted for possible external water mass, in captive dunlin under *ad libitum* feeding conditions. Difference in activity cost = costs on days with rain – costs on days without rain. Gross utilization efficiency = assimilation efficiency  $\times$  efficiency of utilization of metabolizable energy. Solid lines indicate varying energy density of stored body tissue, labeled as the proportion of mass that is fat; dotted lines indicate lower 95% confidence intervals for each energy density.

processing food energy would not be lost, and the factor  $(1-HI)$  would increase or drop out of the first term in the model (Equation 2). This would increase gross energy efficiency, which would increase the significance of differences in activity cost (Fig. 3). The results were sensitive, however, to the possible presence of external water mass. If birds remained dry on rainy days, increases in cost activity were 0.11–0.31  $\text{kJ g d}^{-1}$  less than when estimated by adjusted values (corresponding to 23–100% fat in stored mass), and were significant only if RE was low and gross utilization efficiency was high (cf. Fig. 3).

Mean daily energy expenditure, based on a gross energy

efficiency of 0.64, density of energy stored in body tissue of  $23.61 \text{ kJ g}^{-1}$  and a BMR of  $1.02 \text{ kJ g d}^{-1}$  (Kelly, 2000), was  $2.85 \text{ kJ g d}^{-1}$  or  $2.8 \times \text{BMR}$ . Resting metabolic rate (BMR+TR) averaged  $1.69 \text{ kJ g d}^{-1}$ , or 59% of daily expenditure. Because air temperatures were warmer on days with rain (mean =  $10.7^\circ\text{C}$ ; mean minimum =  $8.1^\circ\text{C}$ ) than on days without rain (mean =  $9.0^\circ\text{C}$ ; mean minimum =  $4.1^\circ\text{C}$ ;  $P < 0.001$ ), resting metabolic rate was reduced slightly on rainy days, by  $0.06 \pm 0.005 \text{ kJ g}^{-1}$  (mean  $\pm$  S.E.M.).

#### Field mass

Stepwise regression identified three weather variables as highly significant predictors of body mass, based on field masses from Bolinas Lagoon corrected for capture-related mass loss and body size (Table 3). Adjusting body masses for possible water retention in plumage on days with rainfall had no effect on which predictors entered the model or on their relative strengths (Table 3). Body mass was significantly lower on days with lower maximum temperatures ( $^\circ\text{C}$ ) and greater wind speed ( $\text{m s}^{-1}$ ), and significantly greater during periods of greater rainfall (cm). Based on adjusted values, body mass ( $\text{g}$ ) =  $26.78 + 8.41 \times \ln[\text{max temperature}] - 0.29 \times \ln[\text{wind speed}] + 0.71 \times \text{rainfall} + 0.01 \times \text{culmen (mm)}$ . Barometric slope was excluded from the model because of an inverse correlation with maximum daily temperature ( $r = -0.65$ ,  $N = 331$ ) and a relatively low  $F$  value. When substituted for maximum temperature in the adjusted model, the partial coefficient suggested an increase of  $1.91 \pm 0.33 \text{ g body mass}$  for each decline of  $100 \text{ Pa h}^{-1}$  in the 12 h slope of barometric pressure (mean  $\pm$  S.E.M., standard partial coefficient = 0.30,  $P < 0.0001$ ). The resulting changes in other predictors were very slight and did not alter their relative influences in the model; the overall strength of the model was reduced only slightly ( $r^2 = 0.22$ ). Increased maximum wind speed was a better predictor of the onset of rainfall the next day ( $F_{1,73} = 18.3$ ,  $P < 0.001$ ) than was increased maximum temperature ( $F_{1,73} = 3.48$ ,  $P = 0.06$ ). Barometric slope did not significantly predict the onset of

Table 3. Stepwise multiple regression of body mass (g) in dunlin banded at Bolinas Lagoon in 1979–1992 (dependent variable,  $N = 354$ ) on daily weather variables

Independent variable	Coefficient $\pm$ S.E.M.	Standard coefficient	$F$	$P$
Maximum temperature ( $^\circ\text{C}$ )				
Adjusted	$8.41 \pm 1.00$	0.48	71.17	$< 0.0001$
Unadjusted	$8.97 \pm 1.00$	0.50	79.74	$< 0.0001$
Maximum wind speed ( $\text{m s}^{-1}$ )				
Adjusted	$-0.29 \pm 0.09$	-0.16	10.96	$< 0.001$
Unadjusted	$-0.30 \pm 0.09$	-0.16	11.66	$< 0.001$
Rainfall (cm)				
Adjusted	$0.71 \pm 0.26$	0.14	7.82	$< 0.01$
Unadjusted	$0.67 \pm 0.26$	0.12	6.72	$< 0.01$

Body mass was corrected for mass loss after capture, body size and intraseasonal trend.

The predictor variables entered for models based on body mass adjusted for possible rainwater retention in plumage ( $r^2 = 0.26$ ) and those based on unadjusted body mass ( $r^2 = 0.27$ ) were the same.



rainfall the next day ( $F_{1,74}=0.02$ ,  $P=0.88$ ) or the same day ( $F_{1,74}=2.34$ ,  $P=0.13$ ). The larger sample of banding masses ( $N=995$ ), which was corrected for body size and possible water in plumage but not for capture-related mass loss, generated the same predictors as the corrected data except that the term for daily rainfall was replaced by daily change (cm) in rainfall ( $b=0.25\pm0.096$ , mean  $\pm$  S.E.M.; standard partial coefficient=0.08,  $P<0.01$ ). Daily change in rainfall and daily rainfall were highly correlated ( $r=0.77$ ,  $P<0.0001$ ).

Field mass of dunlin at Bolinas Lagoon, corrected for body size, intraseasonal trend, and capture-related mass loss, and adjusted for possible rainwater in plumage ( $N=354$ ), were significantly greater on days with rainfall than on days without rain ( $F_{1,349}=28.54$ ,  $P<0.001$ ). The least squares difference was  $2.37\pm0.432$  g (mean  $\pm$  S.E.M.), suggesting a proportional increase of 0.047 on days with rain. Differences based on unadjusted body mass were greater ( $F_{1,349}=39.55$ ,  $P<0.001$ ), with a least-squares difference of  $2.80\pm0.433$  g (mean  $\pm$  S.E.M.), suggesting a proportional increase of 0.055 on days with rain. The larger sample of banding masses ( $N=995$ ), including mass that could not be corrected for capture-related mass loss, produced similar results. Body mass in the larger data set, adjusted for possible water in plumage, was  $0.832\pm0.271$  g (mean  $\pm$  S.E.M.) greater on days with rain ( $F_{1,990}=9.16$ ,  $P=0.002$ ), suggesting a proportional increase of 0.016. Unadjusted mass was  $0.837\pm0.271$  g (mean  $\pm$  S.E.M.) greater on days with rain ( $F_{1,990}=9.27$ ,  $P=0.002$ ), suggesting a proportional increase of 0.017.

### Discussion

Intraseasonal trends in body mass suggested a late December peak only in the aviary birds and no apparent midwinter peak in free-living birds. Both patterns have been observed in dunlin in the UK (Prater, 1975; Pienkowski et al., 1979; Davidson, 1981; Dugan et al., 1981). In British Columbia, dunlin weights showed little fluctuation in November and December, but declined from December/January to March (Kaiser and Gillingham, 1981). In Bodega Harbor, California (Ruiz, 1987), and in Washington state (Buchanan et al., 1985), body mass of dunlin also decreased between December and March. Pienkowski et al. (1979) hypothesized that intraseasonal reductions in body mass might be caused by increasing food scarcity during winter, but body mass declined in captive dunlin, revealing an intraseasonal decline even when birds were supplied with continuously available food. Reductions in body mass might reflect responses to increasing predation pressure (Lima, 1986; Witter and Cuthill, 1993), but the daily pattern of handling which might have been perceived by aviary birds as predation attempts (Lilliendahl, 1997) did not change during the study period.

### Body mass regulation

Dunlin increased their body mass in response to natural and artificial rainfall, indicating that prior to changes in rainfall, birds limited their energy stores to levels below physiological

capacity. In addition, birds undercompensated for daily costs during favorable weather conditions, losing body mass. This is consistent with the hypothesis that birds regulate energy stores to minimize daily cost of excess mass and risk of starvation (Lima, 1986; Witter and Cuthill, 1993), as thermal and foraging conditions vary with passing storms and periods of high freshwater runoff (Dugan et al., 1981; Nordby and Zedler, 1991).

Our results were unclear with regard to wind. Body mass increase in captive dunlin suggested that, in the absence of food limitation, birds may exhibit anticipatory increases in body mass with increasing wind speed. However, inverse correlation with field mass suggested that convective heat loss associated with heavy wind requires use of energy stores (Dugan et al., 1981). Wind speed is not an effective indicator of approaching storms because wind is often strong immediately after as well as in the absence of storms. Southerly winds are associated with the arrival of storms, but wind direction did not enter the regressions of field mass, and could not be accurately measured inside the aviaries. Strong wind may also hinder the detection of prey and therefore reduce energy intake (Dugan et al., 1981; Pienkowski, 1981; Goss-Custard, 1984).

Dunlin incur thermal metabolic costs at ambient temperatures below 20 °C (Kelly, 2000). As with wind speed, lower field mass on days with lower temperatures suggested thermoregulatory limits on daily maintenance of body mass and energy balance in free-living birds. In contrast, captive birds increased their body mass slightly with lower temperatures, independent of rainfall. In either case, however, the occurrence of warmer temperatures on days with rain than on days without rain may have contributed to the ability of birds to increase body mass in response to approaching storms. In a study of seasonal energetics in a California coastal population of white-crowned sparrow *Zonotrichia leucophrys nuttalli*, Weathers et al. (1999) found higher field metabolic rates and lower rates of mass loss on days with rainfall than on days with no rain, even though rainy days were warmer. Our results suggesting increases in maintenance activity and body mass on rainy days are consistent with their results.

Increased solar radiation can reduce thermostatic costs substantially, even under windy conditions (Wiersma and Piersma, 1994; Wolf and Walsberg, 1996). That dunlin reduced their mass with increasing solar radiation suggests adaptive responses to reduced risk of starvation *versus* relative increase in cost of extra mass.

Our results suggest that unless thermal or foraging demands limit the ability of birds to regulate energy balance, dunlin should increase body mass on rainy days. During extended periods of rain, higher costs of foraging, reduced tidal exposure, and increased maintenance costs might limit the ability of free-living birds to regulate their body mass. Although wintering shorebirds in coastal central California commonly experience measurable rainfall (31 % of days in San Francisco from November through March, 1948–2000; Western Regional Climate Center, Reno, Nevada, USA), the proportion of time it is actually raining is generally very small.

Nonetheless, winter rainstorms and runoff are associated with frequent shifts in habitat use and regional movements of shorebirds (Warnock et al., 1995; Kelly 2001). In other temperate coastal locations, rainfall may be less prevalent with relatively little effect on shorebirds.

Average rate of mass gain in dunlin fed *ad libitum* on days with rainfall was  $0.6\text{--}1.4\%$   $\text{d}^{-1}$  ( $0.3\text{--}0.7\text{ g d}^{-1}$  in a 50 g bird). Field mass of free-living dunlin on Bolinas Lagoon suggested a much greater gain of  $4.7\text{--}5.5\%$  on days with rainfall ( $3.0\text{--}3.9\%$ , lower 95% confidence interval; suggesting a minimum increase of  $1.5\text{--}1.9\text{ g d}^{-1}$  in a 50 g bird). The relatively greater differences in the field results could be explained by unmeasured variation in field mass over time intervals longer than a day. However, shorebirds are considered capable of increasing body mass at rates of  $4\text{--}5\%$   $\text{d}^{-1}$  (Zwarts et al., 1990), and gains up to 8.5% have been recorded in dunlin (Dierschke, 1998). We found a daily increase of 3.2% or more 10% of the time in aviary dunlin supplied with continuously available food under natural weather conditions. After a day of enforced fasting and mass loss, aviary dunlin often increased body mass by more than 10% (Kelly, 2000), suggesting that digestive bottlenecks may not constrain substantial daily gains. The contrast with results from captive birds suggests that free-living birds may have regulated energy stores in response to fluctuations of food availability or starvation risk that did not occur in aviary birds fed *ad libitum*. If the colder temperatures between storms were associated with increased predation pressure (Page and Whitacre, 1975) relative to stormy periods that limit shorebird foraging opportunities, then rain-related body mass differences in free-living birds may reflect an inverse correlation between predation and starvation risk. Because of possible sampling error associated with uncontrolled factors, such as the extent of non-feeding time or mass loss prior to capture, or changes in predation pressure, the field masses provide only preliminary evidence of short-term body mass regulation, requiring further investigation in free-living birds.

We found no evidence that dunlin responded to changes in barometric pressure independently of daily changes in rainfall. Perhaps they could not perceive barometric pressure (but see von Bartheld, 1994). Alternatively, the onset of rain may be a more accurate indicator of deteriorating feeding conditions that result from winter storms, especially at latitudes such as Tomales Bay ( $38^\circ\text{N}$ ), where approaching Pacific storms often veer northward before landfall, allowing milder conditions to prevail.

#### Energy use

The energy requirements of free-living birds generally exceed the existence metabolism (EM) of caged birds, because of the costs of foraging, flying to and from roost sites, and avoiding predators (Kendeigh et al., 1977). Although foraging was unnecessary in aviary dunlin, social interaction, occasional group flights, and daily (nightly) capture for weighing probably increased their energy demand over the EM of birds held in small cages. Nonetheless, our estimated metabolic rate of

$2.8\times\text{BMR}$  for dunlin held in  $33\text{ m}^2$  aviaries fell within the range of predicted EM for shorebirds ( $2.2\text{--}3.0\times\text{BMR}$ ) (Kersten and Piersma, 1987), and near values for red knot in a  $50\text{ m}^2$  aviary ( $2.9\text{--}3.9\times\text{BMR}$ ) (Poot and Piersma, 1994).

For an energy density of stored body tissue of  $23.61\text{ kJ g}^{-1}$  (55% fat), the expected rainfall-related body mass increase of  $0.55\text{--}0.95\text{ g}$  in a captive 50 g dunlin under artificial rainfall, or  $0.29\text{--}0.69\text{ g}$  under natural rates of rainfall (values adjusted – unadjusted for maximum likely external water mass), would provide  $6.8\text{--}22.4\text{ kJ}$  of additional stored energy on rainy days. Based on an estimated average daily energy expenditure of  $2.85\text{ kJ g}^{-1}$ , this would provide  $1.1\text{--}3.8\text{ h}$  of additional daily energy support, although values may be smaller if field metabolic rates are higher. If birds deposit more than 55% fat as energy stores, these values would be greater. Such additional reserve energy might enable birds to endure temporary periods of restricted feeding or reduced tidal exposure. When foraging is not possible, birds may concentrate at roosting sites where activity levels and convective heat loss are reduced. In this situation, energy stores would provide longer support than indicated by average daily energy use. Alternatively, additional energy stores accumulated during periods of rainfall may simply compensate for the increased costs of maintenance activities needed to stay dry.

If dunlin flight requires  $17.89\text{ kJ h}^{-1}$ , estimated by the method of Castro and Myers (1988, 1989), additional energy stored on days with rain would provide  $0.4\text{--}1.3\text{ h}$  of additional flight time in a 50 g dunlin. At a cruising speed in dunlin of  $75\text{ km h}^{-1}$  (Warnock and Gill, 1996), this would extend the potential range of hard weather flights by an additional  $30\text{--}97\text{ km}$ . Dunlin apparently fly eastward to escape midwinter declines in the suitability of coastal foraging areas (Warnock et al., 1995; Kelly, 2001). If departing birds take advantage of favorable onshore tail winds, or if heat produced by flight substitutes for thermoregulatory costs (Webster and Weathers, 1990; Bruinzeel and Piersma, 1998), the additional flight range might be considerably farther. Rain-related differences in body mass of free-living birds were substantially greater than increases observed in captive birds. Based on the calculations above, these differences suggested an average increase equal to  $9.3\text{--}10.9\text{ h}$  of daily energy costs, or  $3.3\text{--}3.8\text{ h}$  of additional flight.

Weather was more variable in 1997–98 than in 1998–99, and this variation was reflected by increased variation in body mass in captive dunlin. However, differences in mean body mass were not detectable between years. This suggests body mass responses to each approaching storm rather than general adjustments to mild or harsh winters. Short-term responses to the onset or cessation of rainfall suggest an evolutionary hypothesis, i.e. that natural selection favors shorebirds that first enhance and then reduce energy stores with the passage of winter storms. The precise relationships among potential proximate factors associated with such changes, and whether their use evolved in relation to correlated present or future thermal stress, or indirectly as indicators of future foraging constraint, need further investigation.

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