VARIATION OF BODY MASS IN MOORHENS *GALLINULA CHLOROPUS* WINTERING IN A TEMPERATE AREA

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INTRODUCTION

In birds body mass changes should reflect a trade-off between costs and benefits of energetic storage (Witter & Cuthill, 1993). Benefits include lowered probability of starvation and of thermal stress, while costs include impaired flight of fattened birds and generally higher potential predation risks (Lima, 1986; Rogers, 1987; Gosler *et al.*, 1995). The regulation of body mass can be both exogenous (proximate factors) and endogenous (ultimate factors). Proximate factors affect individuals on a short-term scale, important factors being food abundance (conditioned in turn by physical variables like temperature and snowfall) and thermal dispersion (Dawson & Marsh, 1986; Blem, 1990). Ultimate factors reflect long-term adaptations evolved to match the photoperiod and the climatic conditions in the wintering area of each population (Stokkan *et al.*, 1995).

In temperate and boreal areas birds have to cope with environmental severities, which are particularly evident during winter, and different strategies of winter fattening have been described in resident birds. Lehikoinen (1987) suggested four models of winter fattening, which differ in the amplitude of the daily weight cycle. According to these models a mass increase toward mid-winter must anticipate the adversities (snow, below zero temperature) of the coldest period of the year. The models imply an annual endogenous cycle of fattening, possibly induced by the shortened photoperiod in autumn. In migratory species, the mid-winter peak could be embraced between the two major peaks of body mass observed before the autumn and spring migrations, as reported for songbirds and shorebirds by Scott *et al.* (1994).

A different pattern of winter-survival strategy was described in ducks, where a depletion of the reserves stored in autumn occurs in winter (Reinecke *et al.*, 1982; Whyte & Bolen, 1984; Miller, 1986; Pawlina *et al.*, 1993). Although an endogenous annual cycle of fat deposition was proposed for captive ducks (Loesch *et al.*, 1992), the same phenomenon was not found in natural populations of the Canvasback Duck *Aythya valisineria* (Lovvorn, 1994) and Mallard *Anas platyrhynchos* (Zorn *et al.*, 1995).

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The aim of our study was to describe the pattern of winter fuel store in the Moorhen *Gallinula chloropus*. In a population wintering in a temperate area of North Italy we:

1) analysed the seasonal variations in mass in relation to 19 proximate (short-term) and ultimate (long-term) time and temperature parameters and the photoperiod;

2) assessed the influence of night temperature on the consumption of body reserves in 36 Moorhens exposed to different overnight temperatures;

3) measured indirectly the fat deposits in Moorhens with the non-invasive Tobec system (Castro *et al.*, 1990; Scott *et al.*, 1991) to estimate whether seasonal mass decrease was related mainly to lipid depletion (fat) or to both lipid and protein (body muscles) consumption.

METHODS

The study was carried out at Novi Ligure, along the river Scrivia, during the winters of 1994/95 and 1995/96. The area is in North Italy (100 m a.s.l.) and has a temperate continental climate ("continentale sublitoraneopadano" according to Mennella, 1976). 70 Moorhens in the winter of 1994/95 and 116 in 1995/96 were captured by 6 funnel traps located in an area of 1 km^2 and were marked with numbered metal rings. Field sessions were performed at least weekly, and 12 individuals in 1994/95 and 10 individuals in 1995/96 were recaptured later in the season. Mass was measured with an electronic balance (± 0.1 g accuracy) and standard biometrical parameters were measured to the nearest 0.1 mm (tarsus, foot and bill lengths) and 1 mm (tail, third primary and wing lengths).

The composition of the body was evaluated non-invasively by measurement of its electroconductivity with the Tobec (Total Body Electrical Conductivity) system. This device gives an indication of the lean body mass, since the contribution of lipid tissue to conductivity is negligible (Walsberg, 1988, Castro *et al.*, 1990). 114 Moorhens were measured during the winter of 1995/96. They were placed in the detection chamber (76 mm diameter) of an EM-SCAN SA-3000 Small Animal Body Composition Analyser (EM-SCAN Inc., 3420 Constitution Drive, Springfield, Illinois 62707) for 5-6 sec. and the electrical conductivity index was recorded as: Tobec index = (S - E)/R where S = measurement with the specimen, E = empty measurement, and R = reference number (detailed instructions in the EM-SCAN operator's manual). For each individual the measurement was repeated three times and the average value was employed in statistical analyses.

To assess the effect of night temperature on body mass variation, we kept 36 Moorhens in individual cages during the night following their capture. The birds were exposed to different overnight temperatures (range from 0 to 18 °C), and the body mass of each bird was measured in the evening (at dusk) and again in the morning (at dawn).

The variable chosen to explore the influence of climate on body mass and lean mass index was the air temperature. Rainfall and snowfall occur only occasionally in winter in our study area, thus we could not utilize these variables for regression. We calculated both long- and short-term temperature variables. Long-term temperatures were calculated for each date as the average of its values for 71 years

(from 1900 to 1970). Long-term variation of temperature was defined, day by day, as the standard deviation of the 71-year values. Seven short-term temperature absolute values were calculated as the mean temperature of the cumulative days preceding the capture of each bird (i.e. 1 previous day, 2 previous days, ..., 7 previous days). Moreover, seven short-term temperature deviations were calculated as the difference between the temperatures observed in the days preceding the capture and the expected long-term mean temperature.

The temperature values were supplied by the Natural History Museum of Bra. Although the Bra station is located some distance (75 km) from the Scrivia river, its temperatures accurately represent those of our study area since they are significantly related to those of two stations recently installed near our study area (Lobbi at 25 km N, $r_{279} = 0.846$, $p < 0.001$; Acqui at 32 km SW, $r_{300} = 0.899$, $p < 0.001$).

We performed both single factor and multivariate regression analyses with Systat (Wilkinson, 1992). For the multivariate analysis we first performed a Principal Component Analysis (PCA) on the independent variables. The PCA was utilized to explore the interrelations among climatic variables, which were not expected to be independent of each other, and to extract Factor Scores to be used in a multiple regression analysis with body mass as the dependent variable. Only the variables reaching the 0.10 level of significance in the single regression analysis were considered. In order to account for individual size, all regressions with mass as dependent variable were also computed on size-adjusted body mass (the first factor from a PCA of six body measures was employed for correction, Table I).

TABLE I

Principal Component Analysis of body size variables.

VARIABLE	Factor 1 loadings
Wing	0.916
Third primary	0.852
Tail	0.687
Foot	0.670
Bill	0.666
Tarsus	0.586
VARIANCE EXPLAINED	
Factor 1	54.6 %
Factor 2	17.3 %
Factor 3	11.7 %

RESULTS

SEASONAL VARIATION OF MASS

Figure 1 (upper graph) shows the long-term (71 years) mean daily temperature compared to temperature observed in the winters of 1994/95 and 1995/96. In
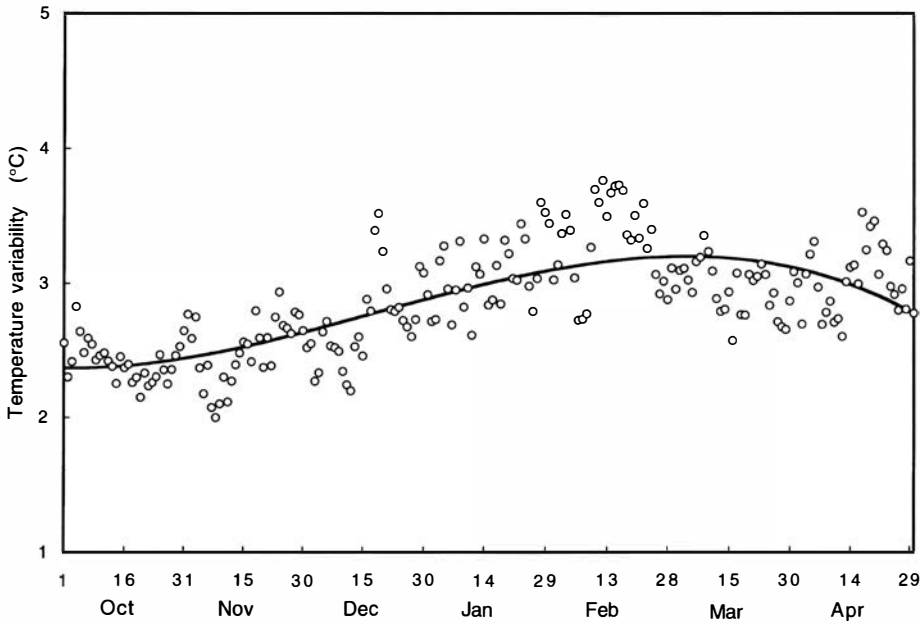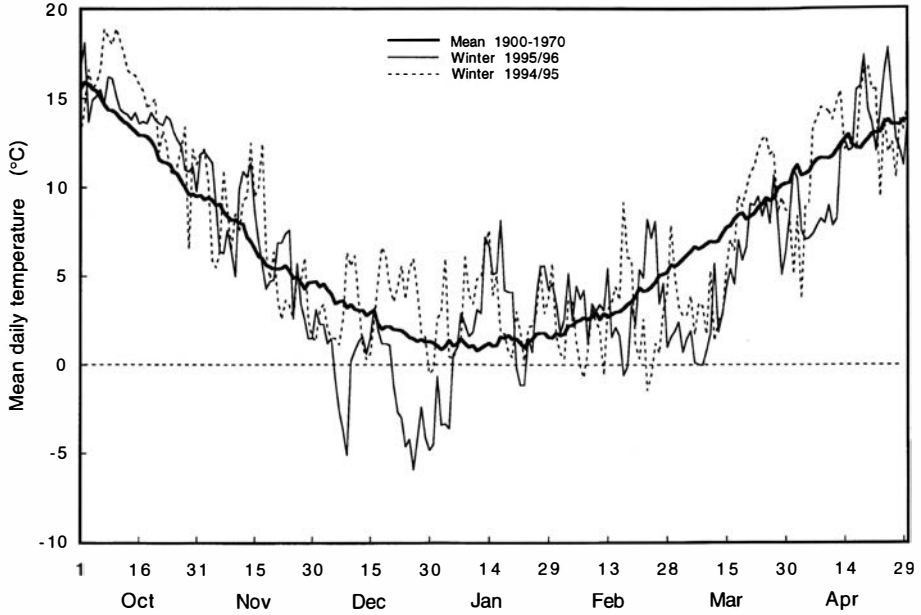
Figure 1. — Temperatures in the study area: upper graph) long-term (71 years) mean daily temperature compared to temperatures observed in the winters of 1994/95 and 1995/96; lower graph) variability of mean daily temperature (S.D. of temperature in the 71 years).

Figure 1 (lower graph) the variability of mean daily temperature (S.D. of temperature in the 71 years) is reported. Mean daily temperature reaches the lowest values at the end of January, while the highest variability is observed in March.

Body mass decreased from early winter to March, from an average of 340 to 250 g, i.e. a decrease of 30 % (Fig. 2). The trend was confirmed by recaptures of several individuals (Fig. 3).

Ten variables out of 19 were correlated significantly with body mass or size-adjusted body mass when considered independently (Table II). Among short-term variables the average temperature of the 2 days preceding capture was most relevant, but also the average temperatures of the 3 to 7 previous days were significantly correlated. None of the deviations between observed and expected temperature were significantly related to body or size-adjusted body mass. All four long-term variables were significantly correlated with body mass, the temperature variability being the most important (Table II).

The variables were not independent of each other. The statistically independent factors were extracted by a Principal Component Analysis; their relationship with the original variables are reported in Table III. The first four factors explained 97.8 % of the variance. Factor 1 was mainly related to the seven short-term temperature variables, Factor 2 to three long-term variables, Factor 3 with the 71-year temperature.
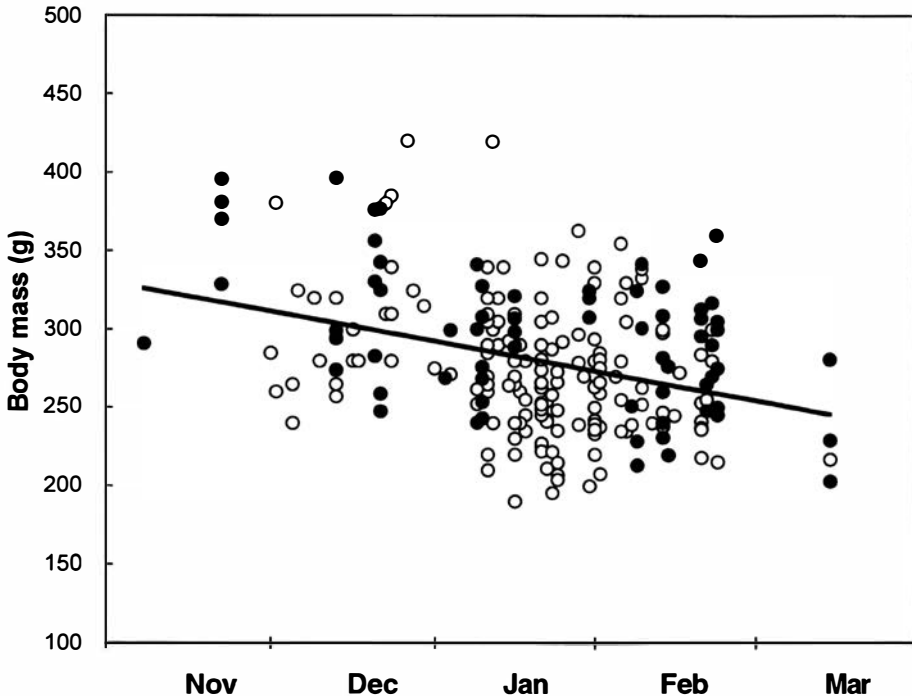

Figure 2. — Seasonal decrease of body mass in the winters of 1994/95 (black dots) and 1995/96 (white dots). Regression line equation: y = 349.6 - 0.635 x; r = 0.337, P < 0.001.
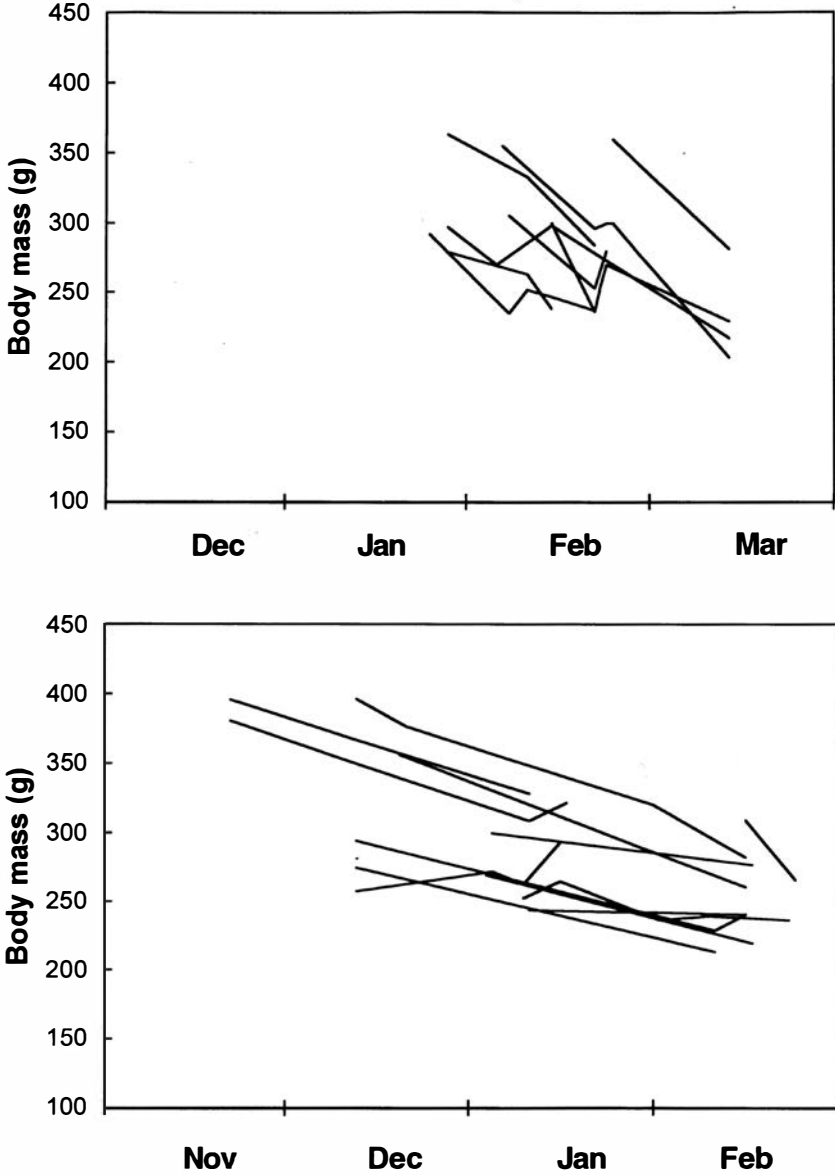
Figure 3. — Body mass decrease of single individuals in a) winter of 1994/95 and b) winter 1995/96.

In the multiple regression analysis, only Factors 1 and 2 were significantly related to mass or to size-corrected mass (Table II). On the whole, the multivariate result is in accord with findings from single-factor univariate regressions and it

TABLE II

Influence of environmental variables on body mass and size-adjusted body mass of Moorhens. N = 186 individuals.

Variables	Body mass		Size-adjusted body mass	
	r	P	r	P
SINGLE-FACTOR REGRESSIONS				
Short-term variables				
Time of capture	0.093	0.208	0.055	0.458
1 previous day temperature	0.120	0.102	0.124	0.095
2 previous days temperature	0.203	0.005**	0.218	0.003**
3 previous days temperature	0.197	0.007**	0.214	0.004**
4 previous days temperature	0.193	0.008**	0.214	0.004**
5 previous days temperature	0.188	0.010**	0.211	0.004**
6 previous days temperature	0.178	0.015*	0.202	0.006**
7 previous days temperature	0.169	0.021*	0.192	0.010**
1 day temperature deviation	0.013	0.863	0.013	0.860
2 days temperature deviation	0.107	0.146	0.122	0.101
3 days temperature deviation	0.105	0.155	0.122	0.100
4 days temperature deviation	0.103	0.162	0.125	0.093
5 days temperature deviation	0.098	0.182	0.126	0.091
6 days temperature deviation	0.087	0.237	0.117	0.114
7 days temperature deviation	0.075	0.309	0.104	0.161
Long-term variables				
Julian date	− 0.393	0.001***	− 0.427	0.001***
71-year mean temperature	0.222	0.002**	0.235	0.001***
71-year temperature variability	− 0.415	0.001***	− 0.454	0.001***
Photoperiod (hours of light)	− 0.391	0.001***	− 0.447	0.001***
MULTIVARIATE REGRESSION				
Factor 1		0.007**		0.002**
Factor 2		0.001***		0.001***
Factor 3		0.095		0.081
Factor 4		0.661		0.219

shows that short- and long-term variables can be successfully grouped in two factors. The multivariate model explained 22.6 % of the variance for mass and 28.2 % for size-adjusted mass.

VARIATION OF BODY MASS IN RELATION TO OVERNIGHT TEMPERATURE

By experimentally exposing Moorhens to different overnight temperatures we observed a negative relation between night temperature and variation of body mass. The experimental individuals lost more mass with low temperatures. The time elapsed from the first measurement (dusk) to the second one (dawn) was positively related to mass variation, while there were no differences between birds of different size (Table IV).

TABLE III

Principal Component Analysis of variables utilized to study daily mass variations. Most important loadings are in italic.

VARIABLE	FACTOR LOADINGS			
	Factor 1	Factor 2	Factor 3	Factor 4
1 day temperature	*0.865*	− 0.119	− 0.352	− 0.294
2 days temperature	*0.935*	− 0.023	− 0.309	− 0.088
3 days temperature	*0.973*	0.001	− 0.186	0.046
4 days temperature	*0.984*	0.031	− 0.064	0.123
5 days temperature	*0.978*	0.037	0.100	0.149
6 days temperature	*0.971*	0.043	0.167	0.120
7 days temperature	*0.961*	0.051	0.198	0.086
Julian date	0.160	− *0.970*	0.038	0.087
71-year mean temp.	0.733	0.372	*0.484*	− 0.232
71-year temp. variab.	0.055	− *0.989*	− 0.020	0.086
Photoperiod	0.105	− *0.912*	0.253	− 0.220
VARIANCE EXPLAINED				
63.1 %	26.5 %	5.8 %	2.5 %

VARIATION OF LEAN MASS INDEX

The seasonal variation of lean mass index observed in the wintering population is reported in Figure 4. There was a decrease of lean mass index from October to March. The magnitude of this seasonal decrease was − 7 %.

DISCUSSION

In our study population the Moorhens were fattest in autumn and there was a significant mass decrease during the winter season. Mass variation in birds during the cold season can follow different patterns: in ducks and ptarmigans, as in Moorhens, the heaviest birds are found in autumn and the mass declines

TABLE IV

Night variation of body mass in relation to temperature. time elapsed between measurements and mass at dusk. N = 36 individuals.

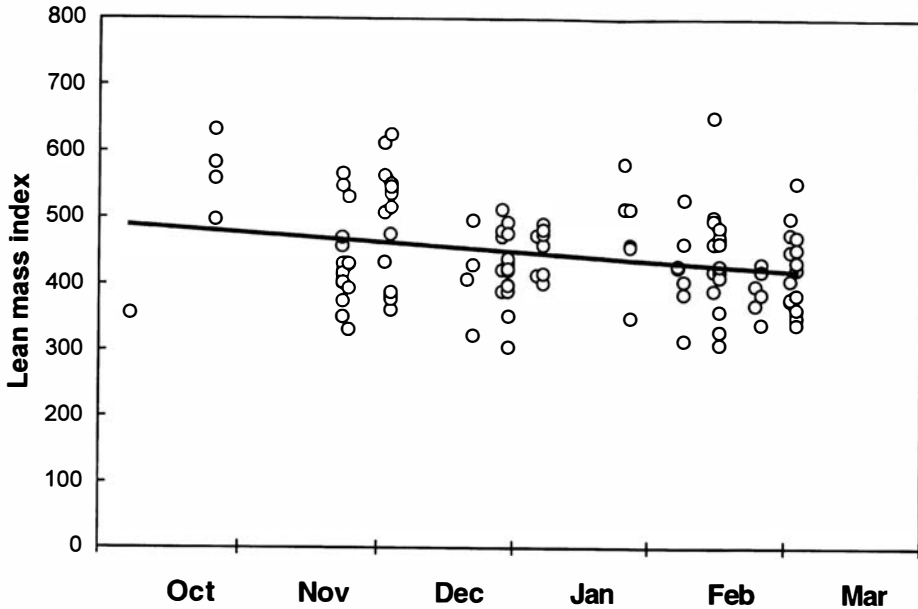| Variables	r	P
Temperature	− 0.366	0.028*
Elapsed time	+ 0.519	0.001***
Mass	+ 0.257	0.131

Figure 4. — Seasonal variation of lean mass index in the winter of 1995/96. Regression line equation: $y = 511.6 - 0.6109 \, x$; $r = 0.246$, $P < 0.003$.

progressively throughout the winter season (Stokkan *et al.*, 1995; Pawlina *et al.*, 1993; Reinecke *et al.*, 1982; Miller, 1986; Zorn *et al.*, 1995; Whyte & Bolen, 1984). In contrast many passerine birds counteract the severity of winter by being fatter in mid-winter (Lehikoinen, 1987; Blem, 1990). Our study is further evidence that the seasonal pattern of fattening is different between non-passerine and passerine birds. However, recent studies have shown that it is not possible to compare the fattening patterns and thermogenic capabilities of these two bird categories: the observed variety of patterns is not strictly linked to phylogeny. For example, in passerines large seasonal changes in body mass and fat stores are common for ground-foraging species, while tree-foraging birds typically show less marked changes (Rogers, 1987; Blem, 1990; Rogers & Smith, 1993). On the other hand, two ecologically similar but unrelated species living in the same area, the White-breasted Nuthatch *Sitta carolinensis* and the Downy Woodpecker *Picoides pubescens,* showed similar cold tolerance, metabolic rate and capacity for thermogenesis (Liknes & Swanson, 1996). In wintering strategies, ecology, environment and geographical distribution play more important roles than phylogeny (Dawson *et al.*, 1983). The winter depletion of fat reserves observed in Moorhens and in ducks is probably related to the similar ecology and size of these birds and not to their belonging to the nonpasserine group (a polyphyletic taxon).

Moorhens lost 30 % of their mass over winter. Similar high values of mass loss have been reported in Canadian and French Mallard populations (Zorn *et al.*, 1995; Pawlina *et al.*, 1993), while in Texan populations the mass decrease was less than 10 % (Whyte & Bolen, 1984). Winter in temperate areas would rarely lead to

high mortality in populations of water birds (for ducks see Whyte & Bolen, 1984; Suter & Van Eerden, 1992), probably making the costs of a true fattening strategy higher than the benefits. In passerine birds the opposite condition would apply (Rogers, 1987; Rogers & Smith, 1993; Witter & Cuthill, 1993), probably because of their small size. Heat loss is more rapid for small endotherms than for large endotherms because of the high surface area to volume ratios of the former (Calder, 1984; Liknes & Swanson, 1996).

It is generally acknowledged that mass variation in birds is mainly due to fat mobilization (Blem, 1990). Many waterfowl species of temperate zones have relatively extensive fat reserves at the beginning of the winter season, much larger than those of passerines (Biebach, 1996). This allows survival times longer than those of passerines in Mallards (Robin *et al.*, 1991), Canada Geese *Branta canadensis* (Raveling, 1979) and Common Coots *Fulica atra* (Visser, 1978). In our study we did not directly measure lipids from dead birds; however the lean mass index obtained by Tobec suggests that also in Moorhens the pattern of reserve depletion is mainly due to fat mobilization. The Tobec index is a reliable indirect measure of lean mass. It has been shown that linear models fit the relationship between Tobec and lean mass for a single species (Walsberg, 1988; Scott *et al.*, 1991). Even if the slope of the relationship between the Tobec index and lean mass differs between species, the slope values found so far are always <1 (range from 0.07 to 0.53 in Scott *et al.*, 1991; from 0.48 to 0.70 in Ash & Roby, 1995; from 0.59 to 0.96 in Lyons & Haig, 1995). Thus we could hypothesize that the decrease of 7 % of the Tobec index over winter accounts for a minor percentage decrease of lean mass. The high (30 %) variation of body mass (lean mass + fat) should be mainly ascribed to depletion of lipid reserves.

The utilization of fat as a primary source of energy during winter is common among birds. It was found in passerines (Blem, 1990), in the Mallard (Whyte & Bolen, 1984) and in the Coot *Fulica atra,* where carcass analysis of starved individuals during severe winters in the Netherlands showed that this rail utilized lipids before body proteins to maintain basal metabolic levels (Visser, 1978).

In many field studies an attempt has been made to establish correlations between environmental factors and the amount of fat. The proximate factors act on the exogenous regulation and the ultimate factors on the endogenous regulation of body mass. In our study the body mass of Moorhens was related both to short-term (birds lose more mass after days with low temperatures) and long-term factors (71-year temperature, photoperiod, for July). Both proximate (short-term) and ultimate (long-term) controls of body mass are likely at work in the population. Similarly, Blem & Shelor (1986) concluded from their multiple regression analysis in the White-throated Sparrow *Zonotrichia albicollis* that long-term (32 years) temperature had an ultimate effect on fat content. Additionally, the temperature over the previous two to three weeks acted as a direct, proximate factor. However, the overall conclusion from many studies on wintering birds is that the size of seasonal fat reserves is more influenced by ultimate than proximate temperature (review in Biebach, 1996). In general it is difficult to conclude from the fact that environmental variables are correlated with fat content that any one of them has a causal effect, their direct effects on mass having not yet been experimentally demonstrated (Biebach, 1996).

Future research could show to what extent the loss of mass in late winter affects the following period of reproduction. Any attribute that improves the chance of mating success should, theoretically, be subject to strong positive

selection. In male Moorhens, good body condition at the beginning of the breeding season has been shown to enhance fitness, because females compete for fat males (Petrie, 1983). For females, body condition affected laying date and clutch size in the Ural Owl *Strix uralensis* (Pietiäinen & Kolunen, 1993) and Kestrel *Falco tinnunculus* (Dijkstra *et al.*, 1988). The gender, the age and the social status of each individual must be carefully considered when the role of fat in winter is evaluated. In some species, dominant individuals carry more fat than subdominant ones (Hogstad, 1987; Verhulst & Hogstad, 1996). However the reverse was found in other studies, where birds of high rank could afford to have lower mass because they had a higher probability of acquiring sufficient food in the future than did subdominant birds (Ekman & Lilliendahl, 1993).

ACKNOWLEDGEMENTS

SUMMARY

The variation of mass during the winter season was studied in a Moorhen (*Gallinula chloropus*) population wintering in North Italy. The influence of 19 short- and long-term time and climatic parameters was evaluated both by single factor regressions and by multivariate analyses. Mass was related positively to the temperature of the days preceding capture and the 71-year mean temperature, and negatively to the date, 71-year temperature variability and photoperiod. Moorhens lost more mass after days with low temperatures and in periods with a high temperature variability. The composition of the body was evaluated by measurement of its electroconductivity with the Tobec system. This device gives an indication of the lean body mass, since the contribution of lipid tissue to conductivity is negligible. During the winter season the Moorhens had a small decrease of lean body mass index suggesting that the consistent weight decrease was due to lipid depletion. By experimentally exposing 36 Moorhens to different overnight temperatures we observed a higher decrease of body mass with lower night temperature. The weight changes in Moorhens did not follow the pattern of winter fattening found in many passerine species. Instead there was a noticeable seasonal decrease of mass (– 30 %) linked to long-term climatic factors and an adjustment of body mass in relation to short-term temperature.

RÉSUMÉ

La variation hivernale du poids corporel a été étudiée dans une population de Poules d'eau (*Gallinula chloropus*) hivernant dans le nord de l'Italie. L'influence de 19 paramètres temporels et climatiques, jouant tant sur le court que le long terme, a été évaluée à la fois par des régressions unifactorielles et des analyses multivariées. Des corrélations positives ont été observées entre le poids et la

température des jours précédant la capture ainsi que la température moyenne sur 71 ans ; les corrélations furent négatives entre le poids et la date de capture, la variabilité de la température sur 71 ans et la photopériode. Les poules d'eau ont perdu le plus de poids après des jours à faible température et durant les périodes à forte variabilité thermique. La composition du corps fut mesurée par électro-conductivité à l'aide d'un système Tobec. Cet appareil donne une indication du poids maigre puisque la contribution des tissus lipidiques à la conductivité est négligeable. Durant l'hiver, les poules d'eau montrèrent une légère chute de l'indice de poids maigre suggérant que la baisse de poids observée était due à l'épuisement des lipides. En exposant expérimentalement 36 poules d'eau à des températures nocturnes différentes, nous observâmes des baisses de poids d'autant plus fortes que les températures nocturnes étaient plus faibles. Les changements de poids des poules d'eau n'ont pas suivi le patron d'engraissement hivernal observé chez beaucoup de passereaux. Au contraire, il y eut une baisse significative (– 30 %) du poids en cette saison, liée à des facteurs climatiques jouant sur le long terme, ainsi qu'un ajustement du poids corporel aux variations à court terme de la température.

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