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THE HEAVIEST NESTLINGS ARE NOT NECESSARILY THE FATTEST NESTLINGS

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Abstract.—Body mass at nest-leaving and subsequent survival, as measured by fledgling recapture and recruitment to breeding populations, are correlated in many species. The hypothesis that nestling body mass and survival are correlated because heavier birds are fatter (i.e., have proportionately greater fat stores) than lighter birds was tested by comparing the fatness of nestling House Wrens (*Troglodytes aedon*) and European Starlings (*Sturnus vulgaris*) of different body masses. As nestling mass and survival after nest-leaving were correlated in the wren population but not in the starling population, it was expected that the heaviest nestlings would be the fattest in House Wrens but not in European Starlings. In neither species were the heaviest nestlings the fattest. These and other published results suggest that the correlation between body mass and survival is attributable mainly to causes other than quantity of relative fat stores, such as differences in degree of maturity or competitive ability.

LOS POLLUELOS MÁS PESADOS NO NECESARIAMENTE SON LOS MÁS GORDOS

Sinopsis.—La masa corporal de los pichones al tiempo de dejar el nido y su supervivencia subsiguiente es correlacionado, en muchas especies de aves, utilizando como parámetro la recaptura de volantones y reclutamiento a la población reproductiva. La hipótesis que la masa corporal y la supervivencia se correlacionan ya que las aves más pesadas deben estar más gordas (ej. tienen proporcionalmente mayor cantidad de grasa almacenada) que las de menor peso, se puso a pruebas comparando la gordura de polluelos de reyezuelo (*Troglodytes aedon*) y de estorninos (*Sturnus vulgaris*). Debido a que la masa corporal de pichones y su supervivencia (luego de dejar el nido) tuvo correlación en la población de reyezuelos, pero no así en la de estorninos, se esperó que los pichones más pesados fueran los más gordos en el reyezuelo pero no así en el estornino. En ninguna de las dos especies los pichones más pesados resultaron ser los más gordos. Este y otros trabajos sugieren que la correlación entre masa corporal y supervivencia no necesariamente tiene que ser atribuida a la cantidad de grasas almacenadas y sí a otras causas tales como la diferencia en el grado de madurez y habilidad competitiva.

In many avian populations, the body mass or condition index of nestlings at or near the time of nest-leaving is positively correlated with their subsequent survival (e.g., Garnett 1981, Hochachka and Smith 1991, Krementz et al. 1989, Loman 1977, Magrath 1991, Nur 1984, Perrins 1965, Tinbergen and Boerlijst 1990). Thompson and Flux (1988) identified three hypotheses that propose a direct causal link between nestling body mass and survival: (1) heavier birds are fatter (i.e., have proportionately more fat) and, therefore, have greater energy stores than do lighter birds (Perrins 1965); (2) heavier birds are more advanced developmentally than lighter birds (O'Connor 1976); and (3) heavier birds are dominant to lighter birds (Garnett 1981). Non-causal explanations for this correlation include that (1) body mass and survival covary independently in response to feeding conditions (Perrins 1988) and (2) parental quality independently influences both body mass and survival (Magrath 1991, Tinbergen and Boerlijst 1990).

A direct test of the hypothesis that greater survival of heavier birds is attributable to greater fat stores is to determine whether the heaviest birds at the time of nest-leaving are the fattest. We examined this question in a House Wren (*Troglodytes aedon*) population in which nestling mass and subsequent survival were correlated (Thompson, unpubl. data) and in a European Starling (*Sturnus vulgaris*) population in which nestling mass and survival were not correlated (Thompson and Flux 1991). We expected that if there were direct causal links in both species between fat stores and survival, the heaviest nestlings would be the fattest in House Wrens but not in European Starlings. We also compared the fat stores in nestling House Wrens with those of fledglings, expecting that fat stores would be depleted during the critical period after nest-leaving.

METHODS

We collected House Wrens in 1986–1987 from a population that had been breeding in nestboxes since 1980 in central Illinois, U.S.A., 40°40′N, 88°53′W (see Drilling and Thompson 1988). House Wrens were collected on brood-days 12–15 (brood-day 0 is the day the first egg of the clutch hatches and nest-departure is on brood-days 14–17) and after they had left the nest. European Starlings were collected on brood-days 20–23, just before they were to leave the nest, at Belmont, New Zealand, 41°10′S, 174°54′E in 1985 (see Flux and Flux 1981).

Birds were weighed prior to collection to determine wet body mass. The frozen carcasses were later thawed and the body cavity opened to remove the stomach contents. The refrozen carcasses were freeze-dried for approximately 96 h. The entire carcass of each House Wren was extracted using petroleum ether. Starlings were ground in a laboratory mixer and about half of the homogenate from each bird was extracted. See Thompson and Flux (1988) for additional details. Fat content was estimated by subtracting lean dry mass and water mass from wet body mass. 'Fatness' was calculated by dividing fat content by wet body mass. Statistical analyses were performed using SAS-PC, version 6.04 (SAS Institute 1987). We used the non-parametric Kruskal-Wallis test (NPAR1WAY procedure) with Tukey follow-up test (GLM procedure using rank scores) and the Wilcoxon two-sample test (NPAR1WAY

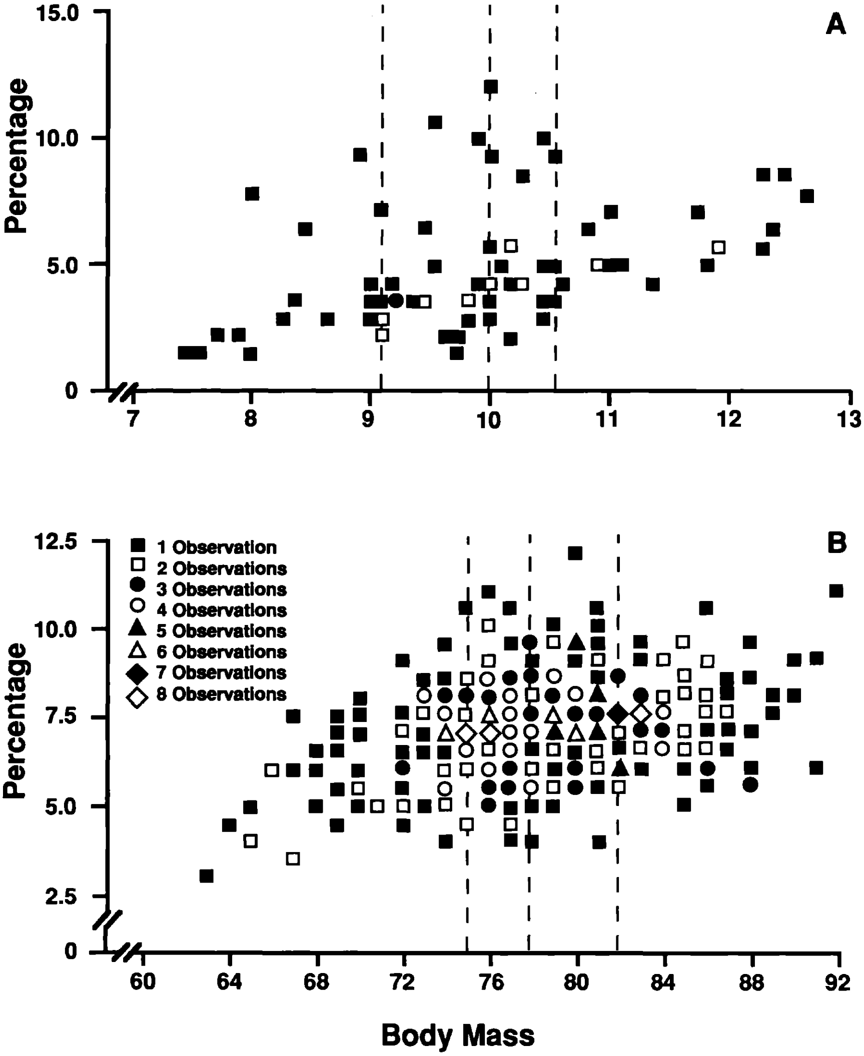

FIGURE 1. Fatness (fat mass divided by wet body mass) of (A) House Wrens and (B) European Starlings in relation to wet body mass near the time of nest-leaving. Vertical lines denote quartiles for body mass.

procedure). The CORR procedure was employed for the Spearman's rank correlation analyses.

RESULTS

Percentage fat at nest-leaving.—In both House Wrens and European Starlings there was a positive correlation between body mass and percentage fat ($r_s = 0.519$, $n = 77$, $P < 0.0001$ and $r_s = 0.252$, $n = 372$, $P < 0.0001$, respectively) (Fig. 1).

TABLE 1. Comparison of fatness (fat mass divided by wet body mass) in House Wren and European Starling nestlings of different body mass quartiles (first = lightest) near the time of nest-leaving. Column medians with the same superscript letter are not significantly different (i.e., $P > 0.05$) based on Tukey follow-up tests of ranks.

	Species					
	House Wren			European Starling		
Quartile	Median	Interquartile range	n	Median	Interquartile range	n
First	2.89[c]	2.36–4.00	20	6.68[b]	5.50–7.48	99
Second	3.71[b,c]	3.22–4.62	20	7.08[a]	6.08–8.14	94
Third	4.54[a,b]	3.99–5.87	18	7.39[a]	6.73–8.06	99
Fourth	5.64[a]	4.86–6.91	19	7.39[a]	6.61–8.20	80

For both species the first (lightest), second, third and fourth quartiles of nestling body mass were determined and the fatness (percentage lipid) of the birds from each quartile was compared. Fatness differed significantly among quartiles in both species (wrens Kruskal-Wallis $\chi^2 = 18.35$, df = 3, $P = 0.0004$; starlings $\chi^2 = 25.57$, df = 3, $P < 0.0001$). The fatness of House Wren nestlings in the fourth and third quartiles and in the second and third quartiles did not differ significantly from each other. Similarly, there was no significant difference in fatness of European Starling nestlings in the fourth, third and second quartiles of the body mass distribution (Table 1). Furthermore, in both species, the fattest nestlings were not among the heaviest quartile (Fig. 1).

Fat stores after nest-leaving.—To investigate the relationship between changes in body composition and age in House Wrens, we compared nestlings collected on brood-days 12–15, when little change in body mass occurs (see Finke et al. 1987), with fledglings recaptured later. Body mass was positively correlated with age ($r_s = 0.197$, $n = 125$, $P = 0.03$), whereas total fat mass was negatively correlated with age ($r_s = -0.186$, $n = 125$, $P = 0.024$). Thus, House Wrens recaptured as fledglings were significantly less fat than nestlings about to leave the nest (Wilcoxon $Z = 4.56$, $P < 0.0001$) (Fig. 2).

DISCUSSION

The expectation that the heaviest nestlings would be the fattest in the House Wren but not in the European Starling was not met. In neither species were the heaviest birds the fattest. Hence, the results from House Wrens are not consistent with the hypothesis that there is a direct causal link between fat stores and survival. Although heavier wrens survived better than lighter wrens after leaving the nest in each of 4 yr (Thompson, unpubl. data), apparently it was not solely because they possessed greater fat stores. The results from the New Zealand population of European Starlings, in which body mass and survival after nest-leaving are not correlated (Thompson and Flux 1991), may indicate that fat stores are important to survival, but only if one assumes that the fattest birds in

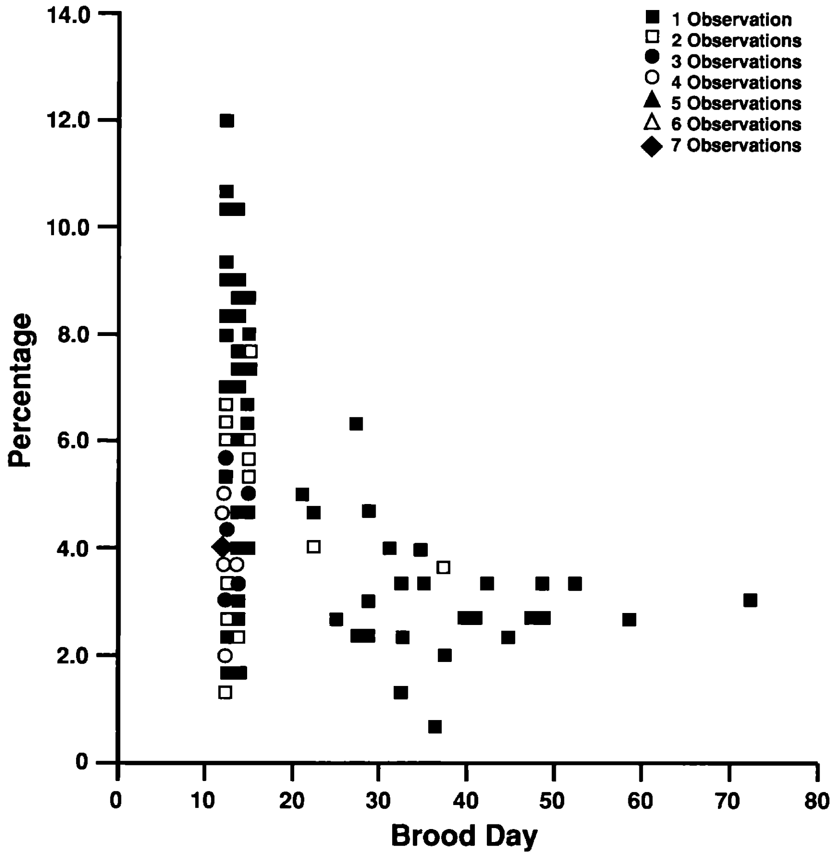

FIGURE 2. Fatness (fat mass divided by wet body mass) of House Wren nestlings near the time of nest-leaving (brood-days 11–15) and fledglings (brood-days >20) recaptured in mist-nets after nest-leaving.

each mass category survived better than those birds with lower fat stores. As the relationship between fat stores of birds about to leave the nest and their subsequent survival has not been determined for this or any other population, this possibility cannot be rejected. Such an explanation is, however, unlikely, because there is no evidence in House Wrens (this study), Great Tits (*Parus major*) (Garnett 1981), and Song Sparrows (*Melospiza melodia*) (Hochachka and Smith 1991) that the greater survival of heavier birds than of lighter birds is attributable largely to their having greater fat stores.

The apparent depletion of fat stores in House Wrens after nest-leaving suggests that fat stores were drawn upon during this period, and such a result is expected if fat stores are playing some role. Although mass and survival are positively correlated, the heaviest birds were not the fattest, which suggests that carrying the largest fat stores is not always necessary for survival. Perhaps in both species during the years studied, average or greater fat stores enabled fledglings, independently of their mass, to survive brief (approx. 1 d) fasts or to reduce significantly the amount of food their parents had to provide over longer periods (Thompson and Flux 1988; C. Perrins, pers. comm.). Thus, whereas some minimal quantity of stored fat may be required to survive difficult times, large mass itself apparently confers advantages for other reasons.

A significant body of evidence indicates that body mass directly influences survival (Hochachka and Smith 1991, Magrath 1991, Tinbergen and Boerlijst 1990), which suggests that future work should focus on determining the causal mechanism. Our results suggest that variation in energy stores is not the underlying mechanism, at least under the conditions to which these two populations were exposed. Garnett (1981) convincingly argued that the greater survival of heavier over lighter Great Tits is best explained by the hypothesis that heavier and larger birds are competitively superior to lighter, smaller birds. That the heaviest House Wrens are not the fattest is consistent with this hypothesis, as well as O'Connor's (1976) suggestion that heavier chicks survive better because they are developmentally more advanced. To our knowledge, however, O'Connor's hypothesis has not been tested.

Studies on Great Tits (Perrins 1965, 1980, 1988; Tinbergen and Boerlijst 1990) and on Blue Tits (*P. caeruleus*) (Nur 1984) suggest that the very heaviest fledglings may survive less well than those of slightly lower mass. We have no evidence for this in House Wrens or European Starlings, but in such situations it would be particularly instructive to compare the fat stores of birds of different body mass. Future work in this area should include measuring fat stores at the time of nest-leaving and subsequent survival. This is now possible for heavier species with an apparatus that allows fat content of living birds to be estimated from measures of conductivity (Castro et al. 1990, Morton et al. 1991, Roby 1991, Scott et al. 1991, Walsberg 1988).

To conclude, there is little evidence to date that the correlation between body mass at the time of nest-leaving and subsequent survival is attributable mainly to differences in fat stores. Additional work, however, needs to be done to test the validity and generality of this conclusion.

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