# THE ALLOMETRIC RELATIONSHIP BETWEEN RESTING METABOLIC RATE AND BODY MASS IN WILD WATERFOWL (ANATIDAE) AND AN APPLICATION TO ESTIMATION OF WINTER HABITAT REQUIREMENTS

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*Abstract.* We examined the allometric relationship between resting metabolic rate (RMR; kJ day$^{-1}$) and body mass (kg) in wild waterfowl (Anatidae) by regressing RMR on body mass using species means from data obtained from published literature (18 sources, 54 measurements, 24 species; all data from captive birds). There was no significant difference among measurements from the rest (night; $n = 37$), active (day; $n = 14$), and unspecified ($n = 3$) phases of the daily cycle ($P > 0.10$), and we pooled these measurements for analysis. The resulting power function ($a$Mass$^b$) for all waterfowl (swans, geese, and ducks) had an exponent ($b$; slope of the regression) of 0.74, indistinguishable from that determined with commonly used general equations for nonpasserine birds (0.72–0.73). In contrast, the mass proportionality coefficient ($b$; y-intercept at mass = 1 kg) of 422 exceeded that obtained from the nonpasserine equations by 29%–37%. Analyses using independent contrasts correcting for phylogeny did not substantially alter the equation. Our results suggest the waterfowl equation provides a more appropriate estimate of RMR for bioenergetics analyses of waterfowl than do the general nonpasserine equations. When adjusted with a multiple to account for energy costs of free living, the waterfowl equation better estimates daily energy expenditure. Using this equation, we estimated that the extent of wetland habitat required to support wintering waterfowl populations could be 37%–50% higher than previously predicted using general nonpasserine equations.

*Key words: allometry, Anatidae, bioenergetics models, body mass, habitat requirements, resting metabolism, waterfowl.*

## Relación Alométrica entre la Tasa Metabólica en Reposo y la Masa Corporal en Aves Acuáticas Silvestres (Anatidae) y una Aplicación para la Estimación de los Requerimientos de Hábitat Invernal

*Resumen.* Examinamos la relación alométrica entre la tasa metabólica en reposo (TMR; kJ día$^{-1}$) y la masa corporal (kg) en aves acuáticas silvestres (Anatidae) mediante la regresión de la TMR con la masa corporal usando valores promedio para las especies obtenidos a partir de datos publicados en la literatura (18 fuentes, 54 medidas, 24 especies; todos los datos son de aves en cautiverio). No hubo una diferencia significativa entre las medidas de las fases en reposo (noche; $n = 37$), activa (día; $n = 14$) y no especificada ($n = 3$) del ciclo diario ($P > 0.10$), por lo que juntamos estos datos para el análisis. La función de poder resultante ($a$Masa$^b$) para todas las aves (cisnes, gansos y patos) tuvo un exponente ($b$; pendiente de la regresión) de 0.74, que fue indistinguible de aquel determinado con ecuaciones generales comúnmente usadas para aves no paserinas (0.72–0.73). En contraste, el coeficiente de proporcionalidad de masa ($b$; y-intercepto de masa = 1 kg) de 422 excedió al obtenido a partir de ecuaciones para aves no paserinas por un 29% a 37%. Los análisis que usaron contrastes independientes corregidos por filogenia no alteraron sustancialmente la ecuación. Nuestros resultados sugieren que la ecuación para las aves acuáticas brinda una estimación más apropiada de la TMR para los análisis bioenergéticos de los anátidos que las ecuaciones generales para aves no paserinas. Cuando las ecuaciones de los anátidos fueron ajustadas con un múltiplo para incorporar los costos energéticos de la vida en libertad, la ecuación de los anátidos brindó mejores estimados del gasto diario de energía. Usando esta ecuación, estimamos que la extensión de humedales requerida para albergar a las poblaciones invernales de anátidos podría ser un 37% a 50% mayor que la predicha previamente usando las ecuaciones generales para aves no paserinas.

## INTRODUCTION

Wild waterfowl (Anatidae) form an important ecological and economic group, for which government agencies spend large sums to conserve wetlands and manage populations (U.S. Fish and Wildlife Service and Canadian Wildlife Service 1986). Waterfowl require similar conservation efforts across species, including protection and restoration of wetlands, management of nesting areas, and maintenance of foraging opportunities in wetland and agricultural habitats. The objectives of these conservation programs are often bioenergetically based, especially where large wintering waterfowl populations are supported (Heitmeyer 1989, Reinecke and Loesch 1996). These programs rely upon the strong relationship between body mass and basal metabolic rate within and among species of birds (Lasiewski and Dawson 1967, Aschoff and Pohl 1970, Calder 1974, Daan et al. 1989), and require conversion of this rate to field estimates of energy requirements, conversion to food requirements using metabolizable energy values of foods, and extrapolation to food needs of the projected wintering waterfowl population. These data are in turn used with estimates of food density in the field (kg ha$^{-1}$) to estimate the amount of various habitats needed to provide enough food to support populations.

The allometric relationship between body mass and metabolic rate in birds has been used to model total daily energy expenditure of individual birds by assuming, for example, that total daily energy cost for free living is some multiple of basal metabolic rate (King 1974, Drent and Daan 1980, Pienkowski et al. 1984, Daan et al. 1990), although research has not settled on a single multiple (Wiens and Farmer 1996). Basal metabolism is best described by a power function, $a$Mass$^b$, where Mass is body mass in kg, exponent $b$ is the slope of the regression line, and $a$ is the mass proportionality coefficient (y-intercept at mass = 1 kg; Schmidt-Nielsen 1984). In actuality, however, what is termed basal, or standard, metabolic rate (Schmidt-Nielsen 1984, Bennett and Harvey 1987) is quite variable depending upon a number of factors. Basal metabolism is best measured on postabsorptive, fully developed, nonreproductive birds at rest in a dark thermo-neutral environment during the rest phase of the daily cycle (McNab 1997, McKechnie and Wolf 2004); however, published estimates vary with the daily cycle (rest or active), season, climate, latitude, diet, body composition, and habitat (Weathers 1979, McNab 1983, 1988, Bennett and Harvey 1987, Dawson and O'Connor 1996, Battley et al. 2001). Therefore, any given estimate cannot necessarily be considered truly basal (i.e., the lowest; Schmidt-Nielsen 1984). Alternatively, Resting Metabolic Rate (RMR) is a statistic that accounts for the conditions under which data are obtained from test animals, rather than implying a true basal rate of energy use (Schmidt-Nielsen 1984, Bennett and Harvey 1987), and we use this term throughout to reflect the varied nature of the published data available to us.

Lasiewski and Dawson (1967), Aschoff and Pohl (1970), and Bennett and Harvey (1987) found that RMR of passerine birds exceeded that of nonpasserines, but others have found no such difference (Prinzinger and Hänssler 1980, Reynolds and Lee 1996, McKechnie and Wolf 2004). There is, however, evidence for differences in relative RMR across nonpasserine families (Zar 1969, McNab 1983, Bennett and Harvey 1987, Kersten and Piersma 1987, Gabrielsen and Mehlum 1989, Bryant and Tatner 1991, Garland and Ives 2000). Therefore, the use of pooled nonpasserine data (Lasiewski and Dawson 1967, Aschoff and Pohl 1970) to determine RMR values expected for specific taxa is probably not justified. We argue, as did Wasser (1986) for Falconiformes, that the allometric relationship between RMR and body mass determined specifically for waterfowl will have greater theoretical value for analyses of functional relationships of this group (Zar 1969, Bryant and Tatner 1991, Ellis and Gabrielsen 2002), and will provide greater utility for guiding waterfowl conservation programs, than would generalized equations derived from many families of nonpasserines. Accordingly, we conducted an allometric analysis of published RMR and body mass data of wild waterfowl, including the tribes *Anatini* (dabbling ducks), *Aythyini* (diving ducks [pochards]), *Mergini* (sea ducks), *Anserini* (geese), and *Cygnini* (swans), to derive a predictive equation for RMR based on body mass. We

then derived estimates of the energy cost of free living and the amount of wetland habitat (ha) required by a hypothetical wintering waterfowl population in California's Central Valley, the most important waterfowl wintering area in the Pacific Flyway (Gilmer et al. 1982). We compared these estimates with those derived by Heitmeyer (1989), which were based on the Aschoff and Pohl (1970) generalized nonpasserine equation. Our results demonstrate the importance of using taxa-specific allometric equations to develop accurate habitat recommendations.

## METHODS

### ALLOMETRIC DATA

We obtained RMR and body mass estimates for 24 wild northern hemisphere waterfowl species of 11 genera, from 54 measurements of ducks, geese, and swans contained in 18 published sources (Appendix). We did not include southern hemisphere waterfowl (Australasian ducks) because they appear to have a lower metabolic rate than that of northern hemisphere species (McNab 2003). We also did not include domestic waterfowl because their metabolism could be influenced in an unknown way by generations of artificial selection (Hayssen and Lacy 1985). We included only published laboratory measurements of RMR for postabsorptive, normothermic birds at rest in the dark and in a thermoneutral environment during the rest (night), active (day), and unspecified (unknown) daily phases. We converted all RMR data, where necessary, to kJ day$^{-1}$. We accepted conversion of mL O$_2$ g$^{-1}$ hr$^{-1}$ to kJ day$^{-1}$ as provided in the cited sources (19.7–20.2 kJ liter O$_2$$^{-1}$), or we used 19.8 kJ liter O$_2$$^{-1}$ when the source had not already converted to kJ day$^{-1}$ (Ellis and Gabrielsen 2002). When published sources provided data in kcal, we assumed kJ = 4.185*kcal (Gabrielsen et al. 1991), and where the source provided RMR as Watts kg$^{-1}$, we converted to kJ day$^{-1}$ with the equation Watt kg$^{-1}$*kg*86.4 kJ day$^{-1}$ W$^{-1}$, where kg is body mass.

### STATISTICAL ANALYSIS
### OF ALLOMETRIC DATA

We first determined if we should limit our analyses to rest phase data, which theoretically should provide the lowest values of RMR. We plotted all available RMR-body mass data for each species, segregated by daily phase, and examined differences among the phases using analysis of covariance (ANCOVA). We then compared RMR during the active and rest phase for the same individual Wood Ducks (Aix sponsa) and Mallards (Anas platyrhynchos) using data from Gavrilov and Dol'nik (1985). For the five species for which we had both active and rest phase data (species pairs), we regressed RMR on body mass to compare respective RMR values.

We did not conduct regression analyses using all available data points (all data; $n = 54$), because the number of RMR measurements varied by species. Instead, we averaged RMR data for each species where $n > 1$ to reduce the risk of disproportionate representation; for species in which $n = 1$, we used that value as an estimate of RMR. This resulted in a single datum for each species ($n = 24$), hereafter referred to as species means. We analyzed these data using two approaches. First, using log-transformed linear models, we regressed species means of RMR on respective log-transformed body mass means (kg) to determine exponents, mass proportionality coefficients, and coefficients of determination ($R^2$). We corrected for systematic bias of the transformations using the method of Sprugel (1983). We conducted separate analyses for taxonomic subsets of (i) all waterfowl, (ii) geese and all ducks, (iii) all ducks, (iv) dabbling ducks, and (v) diving ducks (pochards and sea ducks). Very small sample sizes of geese and swans ($n = 4$ and 2, respectively) precluded separate analyses for these groups.

Second, to account for phylogenetic relationships in these same taxonomic subsets, we calculated independent contrasts (Felsenstein 1985) as implemented in program PDAP (Garland et al. 1993, 1999, 2001, Garland and Ives 2000) using the phylogeny for Anatidae reported by Figuerola and Green (2000: fig. 1). We examined correlations between the values of the standardized contrasts and their standard deviations as a diagnostic to determine if branch lengths (Pagel 1992) were adequate for analysis of the two traits, as recommended by Garland et al. (2001). For the independent contrasts, we report $R^2$ and $F$-values calculated from the regression forced through the origin (Garland and Ives 2000).

For all group comparisons, we used AN-COVA to test for differences in RMR as a function of body mass (kg) among active, rest, and unknown phases, and among taxonomic subsets. We assessed model fit for the species means analyses using studentized residuals, diagonal HAT values, and Cook's $D$ influence statistic (Myers 1986:276–299) using JMP® software (SAS Institute 2001).

## COMPARATIVE ESTIMATES
## OF HABITAT REQUIREMENTS

Heitmeyer (1989) estimated RMR from body mass of individual waterfowl species (not reported) and developed a bioenergetics model to estimate the amount of wetland habitat required to support wintering waterfowl in the Central Valley of California. As the basis of this model, he used the equation of Aschoff and Pohl (1970) for nonpasserines measured during the rest phase of the daily cycle (RMR = $308 \ast MASS^{0.73}$, where RMR is in kJ day$^{-1}$ and mass is in kg). However, relatively small changes in body mass and mass proportionality coefficients could alter model results considerably, particularly when scaled to an area the size of the Central Valley. To evaluate these effects, we used the Heitmeyer (1989) nonpasserine-based model to determine the amount of habitat required by a hypothetical wintering waterfowl population of 3 million ducks, geese, and swans over a period of five months (450 million use-days). We then contrasted this result with estimates obtained using our waterfowl-specific equations, derived as follows.

First, we calculated the average mass of a standard wintering waterfowl in the Central Valley from which to determine RMR. To do this, we calculated the mean mass of the dabbling duck, diving duck, goose, and swan groups from Bellrose (1980) by pooling the mass of each species wintering in the Central Valley (if ≥1.0% of the total) and assuming 80% adults (mass varies by age). We then weighted the estimated mean masses by the percentage of each species and group in the Central Valley population during winter of 2005 (M. Wolder, U.S. Fish and Wildlife Service Sacramento National Wildlife Refuge, unpubl. data). This gave an estimate of 1.3 kg as the mass of a standard waterfowl. Next, we multiplied the resulting estimate of RMR by a factor of 3, following exactly the Heitmeyer

(1989) model to account for the daily energy costs of free living (King 1974), and by the number of use-days to extrapolate from individual energy expenditure to that of the population. We divided this total by the metabolizable energy value of wetland foods (12.5 kJ g$^{-1}$ from the Heitmeyer [1989] model) to yield population daily food consumption. We then converted food consumption to hectares of wetland habitat by dividing population food consumption by 842 kg ha$^{-1}$, which was Heitmeyer's (1989) estimate of food density in wetlands. Finally, we conducted a sensitivity analysis to measure the percentage change in required wetland area resulting from percentage changes (up to ±50%) in model parameters (i) body mass, (ii) mass proportionality coefficient, (iii) exponent, (iv) RMR multiple adjustment for free living, (v) metabolizable energy value of food, and (vi) food density in wetlands (Miller and Newton 1999).

## RESULTS

### ALLOMETRY

Visual inspection and results from ANCOVA ($F_{2,48} = 0.7$, $P = 0.53$) of all data indicated no obvious overall difference in RMR for active, rest, and unknown daily phases (Fig. 1A). Although estimates of RMR during the active phase of individual Wood Ducks and Mallards ranged from 8%–30% higher than during the rest phase (Appendix), regression of RMR on body mass for the five species for which we had both day and night data showed no significant differences between phases ($F_{1,22} = 0.5$, $P = 0.48$; Fig. 1B). Therefore, we used data from all phases to increase sample size for the predictive equations when using species means. The resulting relationships between species means of waterfowl RMR and body mass are power functions, the scatter of species-specific data points are cohesive, and the log plot is a straight line (Fig. 2). Additionally, the waterfowl regression line is higher than the nonpasserine regression line from Aschoff and Pohl (1970).

The mass proportionality coefficients of species means ranged from 417–457 across taxonomic subsets (Table 1). Influence diagnostics indicated that the values for swans, and possibly the Greater Snow Goose (*Chen caerulescens atlantica*), highly influenced model fit for all waterfowl and geese plus ducks (student-
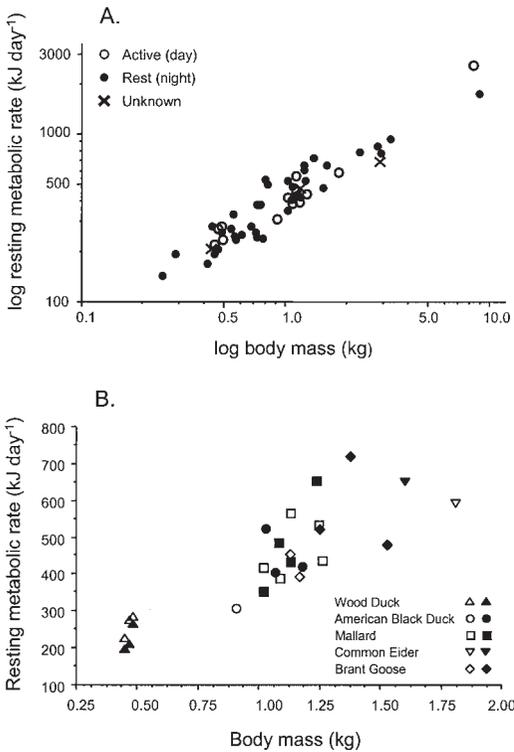
FIGURE 1. Regression of RMR (kJ day$^{-1}$) on body mass (kg) showing: (A) plots of all data for active (day), rest (night), and unspecified (unknown) phases of the circadian cycle for ducks (*Aix*, *Anas*, *Aythya*, *Lophodytes*, *Netta*, *Clangula*, and *Somateria* spp.), geese (*Branta*, *Anser*, and *Chen* spp.), and swans (*Cygnus* spp.); and (B) plots of active (day; open symbols) and rest (night; closed symbols) phases for five species from which data from both phases were available.

ized residuals, diagonal HAT values, and Cook's *D* influence statistic, respectively, are 1.88, 0.27, and 0.64 for Mute Swan; −0.92, 0.28, and 0.17 for Trumpeter Swan; −0.82, 0.10, and 0.18 for Greater Snow Goose). Mass proportionality coefficients for the duck subsets ranged narrowly, from 446–457 (Table 1). Average exponents ranged from 0.71 for geese plus ducks, to 0.98 for diving ducks (Table 1). In all instances, however, the 95% confidence intervals for both exponents and mass proportionality coefficients overlapped among taxonomic subsets. As a result, we found no significant overall differences among regressions using species means ($F_{2,25} = 2.2$, $P = 0.14$). Therefore, the logarithmic equation using species means of all waterfowl provides the

most appropriate estimate of RMR (Fig. 2); however, the all ducks equation could provide an alternative for populations where ducks predominate (Table 1).

When we repeated the analyses using independent contrasts, the $R^2$ and *F*-values decreased markedly except for the diving ducks, which remained similar (Table 1). However, in most instances, the exponents and mass proportionality coefficients remained similar to those of the phylogenetically uncorrected species means data (Table 1). We detected no significant correlations between the values of the standard contrasts and their standard deviations, indicating that the branch lengths we used were adequate for analysis (Garland et al. 2001). The 95% confidence intervals for both exponents and mass coefficients of independent contrasts completely overlapped among groups.

Because of wide 95% confidence intervals (Table 1), we could not distinguish between the average exponents of the waterfowl species means regressions and those determined with the nonpasserine equations of Aschoff and Pohl (1970; 0.73) or Lasiewski and Dawson (1967; 0.72). The latter pooled active and rest phase data, consistent with our analyses. In contrast, the mass proportionality coefficient of the species means equation for the all waterfowl subset exceeded that of the Aschoff and Pohl (1970) nonpasserine equation (308) by 37% and the Lasiewski and Dawson (1967) equation (327) by 29%. The average mass proportionality
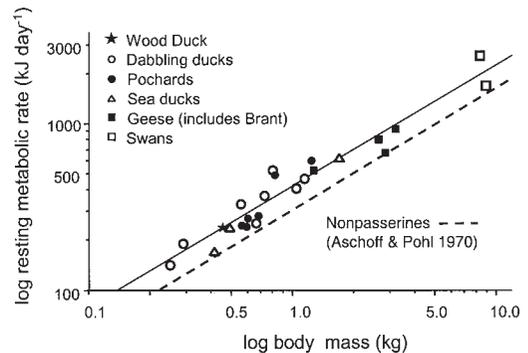


FIGURE 2. Regression of species means of log RMR (kJ day$^{-1}$) on log body mass (kg) for all waterfowl: ducks (*Aix*, *Anas*, *Aythya*, *Lophodytes*, *Netta*, *Clangula*, and *Somateria* spp.), geese (*Branta*, *Anser*, and *Chen* spp.), and swans (*Cygnus* spp.); active (day), rest (night), and unknown phases of the circadian cycle were used.

TABLE 1.   Average exponents (*b*), mass proportionality coefficients (*a*), and statistics from least-squares fitting of the allometric equations resulting from the regression of resting metabolic rate (RMR; kJ day$^{-1}$) on body mass (kg) of wild waterfowl using species means calculated from literature sources (Appendix); active (day), rest (night), and unknown phases of the daily cycle used.

|  | $n^a$ | *b* (95% CI) | *a* (95% CI) | $R^2$ | *F* | df | *P* |
|---|---|---|---|---|---|---|---|
| Species means: | | | | | | | |
| All waterfowl | 24 | 0.74 (0.64, 0.82) | 422 (389, 457) | 0.93 | 299.1 | 23 | < 0.001 |
| Geese + ducks | 22 | 0.71 (0.58, 0.82) | 417 (383, 454) | 0.88 | 148.8 | 21 | < 0.001 |
| All ducks | 18 | 0.84 (0.64, 1.02) | 448 (396, 507) | 0.84 | 83.7 | 17 | < 0.001 |
| Dabbling ducks | 9 | 0.77 (0.46, 1.06) | 457 (368, 567) | 0.84 | 36.6 | 8 | < 0.001 |
| Diving ducks | 9 | 0.98 (0.67, 1.27) | 446 (379, 525) | 0.90 | 59.5 | 8 | < 0.001 |
| Independent contrasts: | | | | | | | |
| All waterfowl | 23 | 0.76 (0.52, 0.99) | 430 (266, 695) | 0.67 | 43.6 | 22 | < 0.001 |
| Geese + ducks | 21 | 0.75 (0.49, 1.01) | 427 (267, 680) | 0.64 | 35.5 | 20 | < 0.001 |
| All ducks | 17 | 0.77 (0.48, 1.11) | 456 (275, 757) | 0.64 | 28.2 | 16 | < 0.001 |
| Dabbling ducks | 8 | 0.68 (−0.30, 1.39) | 439 (154, 1247) | 0.42 | 5.0 | 7 | 0.06 |
| Diving ducks | 8 | 0.92 (0.65, 1.18) | 453 (346, 593) | 0.91 | 68.6 | 7 | < 0.001 |

[a] *n* = number of species.

coefficient for the all waterfowl subset was only 12% lower than that reported by Aschoff and Pohl (1970) for passerines during the rest phase (481).

## COMPARATIVE ESTIMATION OF HABITAT REQUIREMENTS

Based on the model from Heitmeyer (1989), more than 47 000 ha of wetland restoration would be required to meet our hypothetical Central Valley habitat objectives to support 450 million waterfowl use-days (Table 2). However, using the equation we recommend (species means and including all waterfowl), the area increased 37% to over 65 000 ha. Repeating the analysis using the all duck equation resulted in an incremental increase of nearly 50% over that using Heitmeyer's (1989) model (Table 2). The percentage increase in required wetland area was most directly dependent upon the mass proportionality coefficient of the equation. When we used the equations derived from independent contrasts, we found few practical differences in the area of required wetlands compared to that derived from the species means equations (Table 2).

Sensitivity analyses showed that percentage changes in required wetland area varied linearly with percentage changes in mean body mass, mass proportionality coefficient, the multiple of

TABLE 2.   Estimates of wetland area required to support a winter waterfowl population of 450 million use-days in the Central Valley of California, based on allometric equations of Heitmeyer (1989) and the "All waterfowl" equation from Table 1 using species means and independent contrasts.

| Allometric equation | RMR (kJ day$^{-1}$)$^a$ | Energy demand (kJ × 10$^9$) | Food required (kg × 10$^6$) | Wetlands required (ha) | Additional wetlands (ha)$^b$ | Percent increase$^b$ |
|---|---|---|---|---|---|---|
| Heitmeyer (1989) | 373 | 504.1 | 40.0 | 47 516 | – | – |
| Species means (this study): | | | | | | |
| All waterfowl | 512 | 691.5 | 54.9 | 65 176 | 17 660 | 37 |
| All ducks | 559 | 754.1 | 59.9 | 71 076 | 23 560 | 50 |
| Independent contrasts (this study): | | | | | | |
| All waterfowl | 525 | 708.5 | 56.2 | 66 783 | 19 267 | 41 |
| All ducks | 562 | 758.6 | 60.2 | 71 501 | 23 986 | 51 |

[a] Mass proportionality coefficient using standard waterfowl body mass = 1.3 kg; see text.
[b] Additional wetland area compared to Heitmeyer (1989).
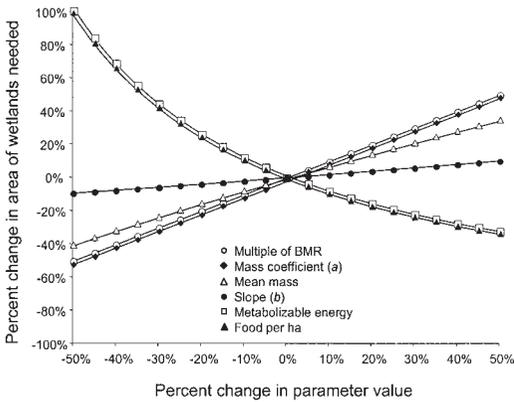
FIGURE 3. Sensitivity analysis showing percentage change in the area (ha) of wetlands required by wintering waterfowl relative to percentage changes of −50% to +50% in six model parameters.

RMR used to account for free living, and the exponent, although the latter had little effect (Fig. 3). Changes in the mass proportionality coefficient and the multiple of RMR had identical, and relatively large, proportionate effects on required wetland area. Percentage change in wetland area varied exponentially with proportionate changes in metabolizable energy of food and food density; reductions in the values of these variables could potentially have larger effects than changes to the other variables (Fig. 3).

## DISCUSSION

### ALLOMETRY

Our results indicate that RMR of wild northern hemisphere waterfowl exceeds estimates from the generalized nonpasserine allometric equations (Lasiewski and Dawson 1967, Aschoff and Pohl 1970), and approaches the RMR of passerines during the rest phase. Zar (1969) also demonstrated a higher RMR for waterfowl using the small waterfowl data set from Lasiewski and Dawson (1967), which included domestic waterfowl. The evolutionary or ecological reasons for differences in metabolic rates among families of nonpasserine birds have not been adequately explained, although a higher RMR is apparently characteristic of northern hemisphere shorebirds (Castro 1987, Kersten and Piersma 1987, Mathiu et al. 1989) and seabirds (Ellis 1984, Gabrielsen and Mehlum 1989, Bryant and Furness 1995, Ellis and

Gabrielsen 2002). This is the general breeding range (Arctic to temperate regions) of the waterfowl species we included in our analysis, and we note that McNab (2003) found that RMR of New Zealand ducks averaged only 70% of that of species endemic to the northern hemisphere. Waterfowl in northern temperate regions could have high RMR to counter potentially greater heat loss associated with the aquatic nature of most species. However, peripheral vasoconstriction compensates to maintain metabolic rates of Common Eiders (*Somateria mollissima*) and Long-tailed Ducks (*Clangula hyemalis*) when the insulative efficiency of their plumage declines while floating in water (Jenssen et al. 1989, Jenssen and Ekker 1989). Also, most waterfowl spend the winter in regions with relatively benign temperatures (Bellrose 1980). Bennett and Harvey (1987) found that after accounting for body mass, which was most influential overall, RMR of seabirds and waterfowl varied with several ecological characteristics, including marsh and marine habitats, aquatic stratification, and foraging methods.

We did not have an independent data set of RMR for northern hemisphere waterfowl against which to test the predictability of our waterfowl equations. We used all extant published data to generate our equations, and even these would benefit from the inclusion of additional swans, large geese, such as the Western Canada Goose (*Branta canadensis moffetti*), and moderate-sized geese, such as Lesser Snow (*Chen caerulescens caerulescens*) and Greater White-fronted Geese (*Anser albifrons*). Future investigations should fill these gaps to reduce confidence intervals around the mass proportionality coefficient estimates in allometric equations, minimize associated biases (McNab 1983, Bennett and Harvey 1987, Reynolds and Lee 1996), and accumulate large independent data sets to facilitate validation tests.

The analyses using independent contrasts to explicitly incorporate phylogeny yielded equations similar to, but with lower predictive ($R^2$) and statistical (*F*-values) power, than did those using uncorrected data. This result is common, although newer phylogenetic analysis techniques provide improved predictive capability (Garland and Ives 2000). Our results suggest that variation in RMR resulted primarily from

variation in body size, rather than from phylogenetic history.

Although RMR estimates for individual Wood Ducks and Mallards during the active phase exceeded those during the rest phase, we could not statistically separate RMR in unknown, rest, and active phases for species means, species pairs, or all data equations. Allometric variation and disproportionate sample sizes masked any phase differences at the taxonomic level (family) of analysis; therefore, we cannot conclude that RMR of northern hemisphere waterfowl differs by phase. Rather, available data suggest there may be no practical differences when combining data from large numbers of species obtained by different investigators in different facilities. However, waterfowl in the wild are active nocturnally and diurnally (Jorde and Owen 1988); therefore, equations based upon RMR which include data from both daily phases may be generally more applicable than those based solely on rest phase data. This is supported by McNab (2003), who found no apparent differences in RMR between rest and active phases in seven of nine southern hemisphere duck species tested, and by Ellis and Gabrielsen (2002), who determined that RMR may not vary by activity phase in some species of seabirds. More research is needed to investigate this issue in waterfowl.

ESTIMATION OF HABITAT REQUIREMENTS

Clarification of the most appropriate RMR equation to use for modeling wintering waterfowl population energy requirements has important practical implications for effective bioenergetics-based habitat planning. When we based the habitat needs of waterfowl in the Central Valley on our all waterfowl species means equation, we observed a large increase in the amount of wetland habitat required to accommodate a hypothetical wintering population, compared to the estimate obtained using Heitmeyer's (1989) original model based on the generalized nonpasserine equation of Aschoff and Pohl (1970). Our analyses demonstrate the ecological and potential financial consequences of bioenergetics-based planning models that are supported by inappropriate allometric relationships between body mass and RMR. Habitat objectives are probably too low in most instances and should be adjusted upwards; expenditures for conservation will have to increase proportionately to meet the new objectives.

Sensitivity analyses showed that the area of wetlands required changed proportionately with changes in the average mass of the standard waterfowl, the all waterfowl equation's mass proportionality coefficient, and the multiple of RMR selected to account for energy costs of free living. Therefore, if the RMR multiple exceeds the factor of 3 used by Heitmeyer (1989), wetland extent and costs will increase proportionately with the increased multiple, and would add to the increase resulting from the revised mass proportionality coefficient. If additional research suggests the multiple for waterfowl should be smaller, then the two parameters would at least partially compensate each other. Additionally, sensitivity results indicate that planners must carefully determine body mass of waterfowl species using their specific areas of interest. The nonlinear relationship between percentage change of food density in wetlands and metabolizable energy value of available foods can have a large effect on wetland area requirements. This result is consistent with the bioenergetics model developed by Miller and Newton (1999) for Northern Pintails (*Anas acuta*). In contrast, even large percentage changes in exponents resulted in only small and inconsequential percentage changes in wetland area.

An alternative to the use of a single multiple of RMR to account for the energy costs of free living is the use of time-activity budgets, in which multiples of RMR are determined for each behavior for the species in question (Weathers et al. 1984). However, obtaining time budget data and energy equivalents for all behaviors on a large number of waterfowl species in the laboratory could prove laborious and costly. The direct use of doubly labeled water (Tatner and Bryant 1989) could provide a straightforward estimate of field metabolic rate; however, this technique requires recovery of test birds, which would be impractical in large multispecies wintering populations. Accordingly, the use of waterfowl-based allometric equations, such as those we have developed, will likely remain the most practical approach to determining wetland requirements during winter for most conservation applications.

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APPENDIX.   Body mass (g) and resting metabolic rates (RMR) of wild waterfowl obtained from literature sources ($n = 54$) during the rest (night), active (day), and unknown phases of the circadian cycle.

| Species | Body mass (g) | RMR (kJ day$^{-1}$) | Phase of daily cycle | $n$ | Source | Published units |
|---|---|---|---|---|---|---|
| Graylag Goose, Anser anser | 3250 | 937 | rest | 1 | Gavrilov and Dol'nik (1985) | kJ bird$^{-1}$ day$^{-1}$ |
| Emperor Goose, A. canagica | 2303 | 781 | rest | 1 | Gavrilov and Dol'nik (1985) | kJ bird$^{-1}$ day$^{-1}$ |
| Emperor Goose, A. canagica | 2800 | 851 | rest | 1 | Gavrilov and Dol'nik (1985) | kJ bird$^{-1}$ day$^{-1}$ |
| Emperor Goose, A. canagica | 2915 | 768 | rest | 1 | Gavrilov and Dol'nik (1985) | kJ bird$^{-1}$ day$^{-1}$ |
| Snow Goose, Chen caerulescens | 2930 | 670 | unknown | 10 | Boismenu et al. (1992) | Watts kg$^{-1}$ |
| Brent Goose, Branta bernicula | 1130 | 454 | active | 1 | Irving et al. (1955) | ml O$_2$ g$^{-1}$ hr$^{-1}$ |
| Brent Goose, B. bernicula | 1168 | 391 | active | 1 | Irving et al. (1955) | ml O$_2$ g$^{-1}$ hr$^{-1}$ |
| Brent Goose, B. bernicula | 1253 | 523 | rest | 4 | Daan et al. (1990) | Watts |
| Brent Goose, B. bernicula | 1379 | 718 | rest | 1 | Gavrilov and Dol'nik (1985) | kJ bird$^{-1}$ day$^{-1}$ |
| Brent Goose, B. bernicula | 1528 | 478 | rest | 1 | Gavrilov and Dol'nik (1985) | kJ bird$^{-1}$ day$^{-1}$ |
| Mute Swan, Cygnus olar | 8300 | 2619 | active | 5 | Bech (1980) | ml O$_2$ g$_{s.w}$$^{-1}$ hr$^{-1}$ |
| Trumpeter Swan, C. buccinator | 8880 | 1749 | rest | 1 | Benedict and Fox (1927) | ml O$_2$ g$^{-1}$ hr$^{-1}$ |
| Wood Duck, Aix sponsa | 448 | 194 | rest | 1 | Gavrilov and Dol'nik (1985) | kJ bird$^{-1}$ day$^{-1}$ |
| Wood Duck, A. sponsa | 448 | 222 | active | 1 | Gavrilov and Dol'nik (1985) | kJ bird$^{-1}$ day$^{-1}$ |
| Wood Duck, A. sponsa | 468 | 206 | rest | 1 | Gavrilov and Dol'nik (1985) | kJ bird$^{-1}$ day$^{-1}$ |
| Wood Duck, A. sponsa | 468 | 273 | active | 1 | Gavrilov and Dol'nik (1985) | kJ bird$^{-1}$ day$^{-1}$ |
| Wood Duck, A. sponsa | 485 | 261 | rest | 1 | Herzog (1930) | kJ bird$^{-1}$ day$^{-1}$ |
| Wood Duck, A. sponsa | 485 | 281 | active | 1 | Herzog (1930) | kJ bird$^{-1}$ day$^{-1}$ |
| Gadwall, Anas strepera | 791 | 536 | rest | 1 | Prinzinger and Hänssler (1980) | kJ bird$^{-1}$ hr$^{-1}$ |
| Eurasian Wigeon, A. Penelope | 539 | 271 | rest | 1 | Prinzinger and Hänssler (1980) | kJ bird$^{-1}$ hr$^{-1}$ |
| Eurasian Wigeon, A. Penelope | 718 | 260 | rest | 1 | Gavrilov and Dol'nik (1985) | kJ bird$^{-1}$ day$^{-1}$ |
| Eurasian Wigeon, A. Penelope | 723 | 244 | rest | 1 | Gavrilov and Dol'nik (1985) | kJ bird$^{-1}$ day$^{-1}$ |
| American Black Duck, A. rubripes | 904 | 309 | active | 1 | Hartung (1967) | kcal bird$^{-1}$ day$^{-1}$ |
| American Black Duck, A. rubripes | 1026 | 523 | rest | 1 | Berger et al. (1970) | ml O$_2$ min$^{-1}$ |

APPENDIX.   Continued.

| Species | Body mass (g) | RMR (kJ day$^{-1}$) | Phase of daily cycle | $n$ | Source | Published units |
|---|---|---|---|---|---|---|
| American Black Duck, *A. rubripes* | 1066 | 405 | rest | 1 | Bennett and Harvey (1987) | kcal bird$^{-1}$ day$^{-1}$ |
| American Black Duck, *A. rubripes* | 1180 | 422 | rest | 1 | Wooley and Owen (1977) | kcal kg$^{-1}$ day$^{-1}$ |
| Mallard, *A. platyrhynchos* | 1020 | 352 | rest | 1 | Gavrilov and Dol'nik (1985) | kJ bird$^{-1}$ day$^{-1}$ |
| Mallard, *A. platyrhynchos* | 1020 | 416 | active | 1 | Gavrilov and Dol'nik (1985) | kJ bird$^{-1}$ day$^{-1}$ |
| Mallard, *A. platyrhynchos* | 1081 | 485 | rest | 1 | Prange and Schmidt-Nielson (1970) | L O$_2$ kg$^{-1}$ hr$^{-1}$ |
| Mallard, *A. platyrhynchos* | 1084 | 387 | active | 1 | Smith and Prince (1973) | kcal bird$^{-1}$ d$^{-1}$ |
| Mallard, *A. platyrhynchos* | 1132 | 435 | rest | 1 | Gavrilov and Dol'nik (1985) | kJ bird$^{-1}$ day$^{-1}$ |
| Mallard, *A. platyrhynchos* | 1132 | 567 | active | 1 | Gavrilov and Dol'nik (1985) | kJ bird$^{-1}$ day$^{-1}$ |
| Mallard, *A. platyrhynchos* | 1166 | 461 | unknown | 1 | Bennett and Harvey (1987) | kcal bird$^{-1}$ day$^{-1}$ |
| Mallard, *A. platyrhynchos* | 1236 | 655 | rest | 1 | Prinzinger and Hänssler (1980) | kJ bird$^{-1}$ hr$^{-1}$ |
| Mallard, *A. platyrhynchos* | 1248 | 535 | active | 1 | Smith and Prince (1973) | kcal bird$^{-1}$ day$^{-1}$ |
| Mallard, *A. platyrhynchos* | 1263 | 438 | active | 1 | Hartung (1967) | kcal bird$^{-1}$ day$^{-1}$ |
| Northern Shoveler, *A. clypeata* | 554 | 335 | rest | 1 | Prinzinger and Hänssler (1980) | kJ bird$^{-1}$ hr$^{-1}$ |
| Northern Pintail, *A. acuta* | 721 | 377 | rest | 1 | Prinzinger and Hänssler (1980) | kJ bird$^{-1}$ hr$^{-1}$ |
| Garganey, *A. querquedula* | 289 | 193 | rest | 1 | Prinzinger and Hänssler (1980) | kJ bird$^{-1}$ hr$^{-1}$ |
| Eurasian Teal, *A. crecca crecca* | 250 | 144 | rest | 1 | Prinzinger and Hänssler (1980) | kJ bird$^{-1}$ hr$^{-1}$ |
| Red-crested Pochard, *Netta rufina* | 1237 | 613 | rest | 1 | Prinzinger and Hänssler (1980) | kJ bird$^{-1}$ hr$^{-1}$ |
| Common Pochard, *Aythya farina* | 816 | 503 | rest | 1 | Prinzinger and Hänssler (1980) | kJ bird$^{-1}$ hr$^{-1}$ |
| Ring-necked duck, *A. collaris* | 682 | 284 | rest | 1 | McNab (2003) | ml O$_2$ hr$^{-1}$ |
| Ferruginous Duck, *A. nyroca* | 436 | 204 | unknown | 1 | Bennett and Harvey (1987) | kcal bird$^{-1}$ day$^{-1}$ |
| Ferruginous Duck, *A. nyroca* | 440 | 283 | rest | 1 | Prinzinger and Hänssler (1980) | kJ bird$^{-1}$ hr$^{-1}$ |
| Ferruginous Duck, *A. nyroca* | 754 | 377 | rest | 1 | Bennett and Harvey (1987) | kcal bird$^{-1}$ day$^{-1}$ |
| Ferruginous Duck, *A. nyroca* | 780 | 241 | rest | 1 | Bennett and Harvey (1987) | kcal bird$^{-1}$ day$^{-1}$ |
| Tufted Duck, *A. fuligula* | 574 | 234 | rest | 1 | Prinzinger and Hänssler (1980) | kJ bird$^{-1}$ hr$^{-1}$ |
| Tufted Duck, *A. fuligula* | 611 | 253 | rest | 6 | Daan et al. (1990) | Watts |
| Lesser scaup, *A. affinis* | 562 | 248 | rest | 1 | McNab (2003) | ml O$_2$ hr$^{-1}$ |
| Common Eider, *Somateria mollissima* | 1810 | 588 | active | 7 | Jenssen et al. (1989) | Watts kg$^{-1}$ |
| Common Eider, *S. mollissima* | 1600 | 649 | rest | 12 | Gabrielsen et al. (1991) | ml O$_2$ g$^{-1}$ hr$^{-1}$ |
| Long-tailed Duck, *Clangula hyemalis* | 490 | 237 | active | 6 | Jenssen and Ekker (1989) | ml O$_2$ g$^{-1}$ hr$^{-1}$ |
| Hooded merganser, *Lophodytes cucullatus* | 413 | 169 | rest | 1 | McNab (2003) | ml O$_2$ g$^{-1}$ hr$^{-1}$ |