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AN INDIVIDUAL-BASED MODEL TO ESTIMATE THE DAILY ENERGETIC COST OF GREATER RHEAS AND ITS CONTRIBUTION ON POPULATION RECRUITMENT

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ABSTRACT. An individual-based model for estimating the energetic costs in *Rhea americana* was developed considering their sexual and seasonal differences in the behavioral activities. The model includes as variables the individual's characteristics, as well as corporal weight, the time spent on different activities, and the cost associated with each activity. We estimated the daily energetic demand of an adult rhea based on the activities individuals normally develop during postreproductive, nonreproductive, and reproductive seasons, differentiating between sexes. The time spent in each activity for one given animal was calculated from field observations of individuals and the estimations of energetic costs for each activity were obtained from specialized literature. The model built varied between sexes because males and females have different reproductive costs. Both models have the same general formulation but they differ in the cost associated with reproduction. In Greater Rheas, while males assume all of the incubation, the females only lay eggs communally in a single nest. Also the possibility that the individual reproduces or not was considered. The model does not allow to determine whether the energetic costs associated with the breeding are the reason why few individuals try to reproduce but it indicates that there is a clear difference in the daily energetic costs of individuals which reproduce and those which do not reproduce. Other activities associated with parental care posthatching, not taken into account here, would increase these differences, and would explain the low number of breeding attempts observed at wild.

KEY WORDS: Energetic costs, individual behavior, *Rhea americana*, reproductive costs.

1. Introduction. The Greater Rhea, *Rhea americana*, is a native, flightless species that inhabits the open plains of South America, ranging from the south

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of the Amazon River in Brazil to northern Patagonia in Argentina (Handford and Mares [1985]). It is one of the oldest and largest birds in America. The male can measure up to 150 cm in height and weigh up to 35 kg, while the female reaches 130 cm and 25 kg, respectively (Cajal et al. [1993]). The mating system of rhea combines polygyny and sequential polyandry (Bruning [1974]). The male monopolizes a group of females which he mates. Females lay their eggs in a communal nest that is built by the male. The male rolls and incubates the eggs during a period of about 38 days, and then takes care of the chicks or "charos" until they are 2 to 4 months old. Greater Rhea males practically do not leave the nest while incubating (Bruning [1974], Fernández and Reboreda [1998, 2003]). The size of the nest depends on the number of females that form the harem, generally six to eight. However, harems with any number between 2 and 15 females can be observed (Bruning [1974]). Females may mate and lay eggs sequentially in nests of different males. Therefore, the participation of the female is restricted to laying the eggs (Bruning [1974], Bruning and Dolensek [1986]).

A study on reproductive success in the Humid Pampas in Argentina shows that in rhea populations less than 20% of males attempt to reproduce during a breeding season (Fernández and Reboreda [1998]). Most surprising is that only 5 to 6% of the males breed successfully each year. Reproductive success is low for females too, since only some 10% of eggs produce chicks that can reach the age of 3 months. Furthermore, assuming an average harem size of five to six females and no sequential polyandry, approximately 30% of the females breed successfully each year (Fernández and Reboreda [1998]). Fernández and Reboreda [1998] suggest that the low proportion of reproductive males of Greater Rhea and their low reproductive success are a consequence of the high energetic cost of the reproduction. Therefore, a rhea may breed successfully if during the non breeding season it is able to accumulate the energy necessary to face the costs of breeding and parental care.

Our objective is to build an individual-based model for estimating the energetic cost of Greater Rhea focusing on the individual's behavioral pattern. These patterns depend not only on the season, and the natural differences between reproductive and nonreproductive individuals, but also on the individual preferred activities (restless to sedentary animals). Note that here we are not performing an energetic balance which would require knowing how much food the bird consumes, depending on weight, sex and season, the individual's metabolism, and the food's energetic value. Computing energetic balances would require data or studies on weight gain. The estimation of energetic costs allows us to infer why few Greater Rhea individuals would attempt to reproduce and still fewer may breed successfully.

2. Materials and methods

2.1. Field observations.

Field observations were conducted from 1995 to 1999 in two adjacent cattle ranches in the eastern Argentinean Pampas, in the

Province of Buenos Aires, Argentina (36°25′S, 56°56′W). These are open grasslands (<10 m elevation), with homogeneous short pastures grazed mainly by cattle, and with scattered marshes and small patches of woodlands (Soriano et al. [1991]). The ranches cover an area of approximately 4300 ha, and support a Rhea population of roughly 400 individuals. There were no natural predators of adult rheas present (i.e., cougar, *Felis concolor*) but rheas may be occasionally hunted by feral dogs (*Canis lupus familiaris*) and humans (Fernández and Reboreda [1998]).

The activity of individuals in the study area was video-recorded (Sony Hi8 Camcorder, Sony Corp., New York, USA), at distances of 100–200 m between hours 07:30 to 19:30, from a vehicle. Observations involved focal groups of 1 to 12 individuals. Video-recording began 15–20 minutes after arriving where birds were found, allowing the animals to become accustomed to the presence of the vehicle. Recording was done at different sites each day to avoid sampling the same group, though birds were not marked and could move freely within the study area. Hence, repeated observations of the same birds from day-to-day may have occurred occasionally. Recordings were made for up to 10 minutes or until the focal animal moved out of sight or until any bird in the group showed signs of being disturbed. For the activity analysis, recordings shorter than 3 minutes were excluded. The mean length of recordings was 430 seconds (SD 151, range 187–635 s, $n = 173$ recordings). Video-tapes were analyzed with Etholog 2.5.2 (Ottoni [2000]). From each video-tape we arbitrarily chose one or two individuals and analyzed the time spent in different behavioral activities (see below). The percentage of time spent in each activity, its frequency of occurrence, and the mean duration were thus estimated. During censuses and observations of individuals, every courtship and aggressive display was also recorded, and the sex (or age) of individuals involved in the aggression noted. Observations of different individuals within the same group were avoided, except in groups of more than four birds in order to reduce the possibility of pseudoreplication.

Seven behavioral categories were defined: feeding or foraging, vigilance, walking, resting, preening, courtship, and aggression. These categories follow those described by Raikow [1968, 1969], Bruning [1974] and Codenotti and Alvarez [2001]. Feeding and walking are not exclusive behaviors, as rheas move continuously as they forage. We thus considered birds to be "walking" only when they were moving with their heads leveled with or higher than the body. Birds were considered vigilant when an individual stood with its head up, with its neck either stretched or forming an S above its body. An animal was considered resting when the behavior involved crouching and resting postures (Raikow [1968]). A bird was considered preening when standing and inserting its bill among the feathers of wings or body, or pecking at its own neck or legs. Aggression involved threat displays, pecking, chases, and fights (Raikow [1968], Bruning [1974]).

2.2. The model. The energy that an individual can accumulate over 1 day depends, on the one hand, on the assimilated energy and, on the other hand, on

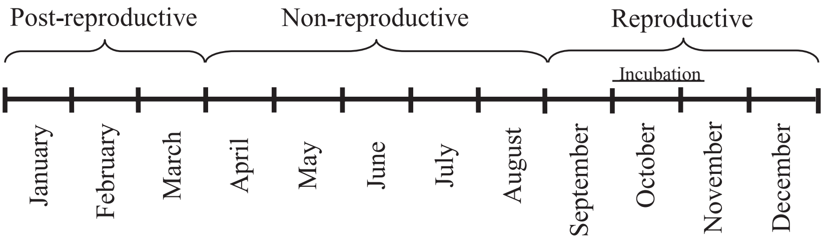

FIGURE 1. Duration of the three seasons in which was divided the year (postreproductive, nonreproductive and reproductive) and the incubation period. The 38-day period can be located anywhere inside the reproductive season, however with different probability.

the spent energy. Moreover, the energy that an individual assimilates depends on food type, rate of consumption, and its capacity to assimilate the different components or nutrients. The adult individual's daily energetic cost (field metabolic rate, FMR, measured in kJ/d) includes the costs of maintenance (basal metabolic rate, BMR), and the costs of locomotion, feeding, reproduction as well as other less intensive activities. BMR represents the minimum energy that an individual needs for supporting the basic functions (breathing, circulation, etc.) within the thermoneutral range. Growth is not considered in our computations because only adult individuals breed. Changes in weight reflect accumulation or consumption of fat reserves.

Data on the BMR and the FMR for some species can be found in the literature. Also, different allometric functions based on the weight of the individuals have been constructed from data such as these (e.g., Grawford and Lasiewski [1968], Nagy [1987], Maloney and Dawson [1993], Tieleman and Williams [2000]). These equations are frequently used for estimating energetic costs for species for which such measurements have not been made.

Alternatively, FMR can be estimated using the time that one individual assigns to each activity, and the energetic cost that this activity has. Here we construct a model considering the time that one bird assigns to the different activities, the photoperiod of the days of the observations, and also the range of weights that adults exhibit during the different seasons. Due to the fact that the individuals exhibit distinct behavioral patterns during each segment of the cycle (Carro and Fernández [2008]), the year was split into three seasons: postreproductive (January–March), nonreproductive (April–August) and reproductive (September–December) (Figure 1 and Table 1).

The field observations were used for estimating the time that an individual dedicated to each activity over a day. In the model, each observation represents the behavior of one individual along 1 day. In the simulations, one observation made

TABLE 1. Portion of the day that non reproductive male and female individuals dedicate to the various activities during different seasons.

		Mean portion of the day assigned to each activity			
Sex	Season	Foraging	Preening, aggression and vigilance	Locomotion	Rest during the day
Female	**Post reproductive**	0.780	0.103	0.115	0
	Non reproductive	0.807	0.093	0.098	0
	Reproductive	0.728	0.082	0.2	0
Male	**Post reproductive**	0.783	0.115	0.102	0
	Non reproductive	0.792	0.099	0.109	0
	Reproductive	0.615	0.179	0.158	0.031

during the corresponding season was randomly assigned to each individual each day.

The daily energetic investment or FMR was estimated, using the field observations, as the sum of the product between the time that the individual assigns to each activity and its energetic cost which also included maintenance costs (Simoy [2011]). This can be written as the vector product of two vectors, B and C, where B is the vector associated with behavior, and C is the vector of the costs of each activity. Each component of B, t_i, is the portion of day assigned to activity i ([h/d]) and each component of C, c_i, is the energetic cost of activity i ([kJ/h]). The cost of reproduction is added as RC, and takes the null value during non reproductive and post reproductive season. RC will be defined further on. The following equation expresses FMR for 1 day

$$FMR(B, C) = \sum_{i=1}^{n} t_i \cdot c_i + RC = \langle B|C\rangle + RC$$

For modeling purposes, the activities were grouped into five categories: (1) preening, aggression and vigilance, (2) rest during the day, (3) locomotion, (4) feeding or foraging, and (5) rest during the night. Vector B, in this case, has five components t_i. It is clear that the first four activities require the light of the day, while the last one takes place in the dark, so that the photoperiod has to be taken into account. Thus, the first four components are obtained from the proportion of day assigned to activity i multiplied by the photoperiod while the last component is the length

TABLE 2. Cost associated with each activity.

Activity	Locomotion and feeding ([v] = km/h, [activity] = ml O_2/g]	Preening, aggression and vigilance, ([activity] = kJ/kg h)	Rest during the day and the night, ([w] = kg, [activity] = kJ/d)
Cost	$0.34 \times v + 0.39$	$1.1 \times RMR$	$1 \times RMR$

of the night, so 24 minus the photoperiod. Our observations allow inferring that the individual remains at rest when it is dark. Because of this, B will depend on Julian day d, so we have $B(d)$.

The costs associated with each category (Table 2) were estimated using repose metabolic rate (RMR)-based equations obtained from a study carried out for ostriches (Williams et al. [1993]). The locomotion cost and RMR for rheas was estimated from Taylor et al. [1971]. The night repose cost is assumed to be the RMR. Consequently, vector C has five positive components too, each c_i being the energetic cost associated with activity i. Since RMR depends on the bird's weight (W), and the cost associated with feeding and locomotion depend on the velocity of displacement during foraging (v_f) and locomotion (v_l), vector C will depend on W, v_f and v_l. This means that the cost C depends both on the individual's activity pattern and on the Julian day (photoperiod) and, because costs are associated with the weight of the individual which is not constant, we have $C(d,\ W,\ v_f,\ v_l)$. Since the cost of each activity depends on the bird's weight, as a first approximation a weight was assigned to each individual for each season, as explained below. The weights of reference were obtained from a rhea population in captivity (M.V. S, unpubl. data).

The daily energetic costs are added over a full year for estimating the yearly accumulated energetic cost for each adult individual not engaged in reproduction (RC $\equiv$ 0). Since BMR and FMR are given in terms of daily costs, this yearly accumulated energetic cost is then divided by the length of the year to obtain average daily energetic costs, using

$$FMR_a\,(B, C) = \frac{1}{365}\left(\sum_{d=1}^{365}\left(\langle B(d)|C(d, W, v_f, v_l)\rangle + RC\right)\right)$$

where: $B(d)$ and $C(d,\ W,\ v_f,\ v_l)$ are the vectors B and C for Julian day d, respectively. It is important to keep track of the Julian day because the photoperiod changes from day-to-day and so does the time assigned to each activity since the behavior is assigned during a portion of the day.

As mentioned earlier, the reproductive costs for females and males were estimated separately since the cost associated with the reproduction is different for each sex. In the case of females, reproductive costs include the development of reproductive structures and the energetic content of the egg. For the males, they are associated with the seasonal testicular growth, the production of sperm, and the cost of the incubation and parental care posthatching.

The energetic content of the ovary and oviduct $[E_0]$ is directly related to the body size of the female $[W]$ (Walsberg [1983]) according to the relationship

$$E_0(W) = 427.1424 \cdot W^{0.938}$$

where $[E_0] = \text{kJ}$ and $[W] = \text{kg}$.

The average weight of a rhea egg is 0.618 kg (Fernández and Reboreda [2008]). This is approximately 2.5% of the corporal weight of an adult female. Walsberg [1983] suggests that the average energetic content of eggs of precocial birds is 7760 ± 1560 kJ/kg. Thus, the cost of producing an egg,$C_e(W)$ is given by

$$C_e(W) = \frac{7760 \cdot 2.5 \cdot W}{100} = 194 \cdot W$$

where $[W] = \text{kg}$ and $[C_e(W)] = \text{kJ}$.

Then, the total cost of reproduction for females $RC(n, W)$ is given by

$$RC\,(n, W) = E_0(W) + n \cdot C_e(W)$$

where n is the number of eggs and $[RC(n, W)] = \text{kJ/d}$. A female can mate with up to three males and she can lay between six and eight eggs per male (Coddenotti [1997]), so, during a breeding season, an adult female may lay 24 eggs at the most.

Regarding the males, Walsberg [1983] has suggested that daily energetic costs of the seasonal testicular growth in birds are smaller than 2% of BMR, and hence it has been considered negligible. Ricklefs [1974] estimated that the necessary energy for the production of semen is 0.8% of BMR, hence it is also negligible. For an individual weight in the range from 30 to 35 kg the 3% of the bird's BMR falls within the range from 70 to 80 kJ/d.

The most important energetic costs are generated once the male has mated and begins incubating the eggs. The cost of incubation is given by the energy that the male must invest in maintaining the temperature of eggs. It was estimated using the Kendeigh equation (Kendeigh [1963]) which calculates the energy needed to keep the temperature of the eggs within the normal range of incubation (34–36 °C). The equation is

$$M = n\,.w.c.b.\,(T_e - T_{na})\,.t.\,(1 - s.pc)\,.10^{-3}$$

where n is the number of eggs in the nest, w is the average weight of the egg (kg), c is the specific heat of the egg (kJ kg^{-1}°C^{-1}), b is the cooling rate of the egg (°C h^{-1}°C $^{-1}$), T_e is the egg temperature (°C), T_{na} is the nest air temperature (°C), s is the proportion of the surface of the egg covered by the incubating bird, pc is the proportion of time that the bird remains at the nest and t is the time interval in hours (24 hour if energetic cost is estimated for a day).

The cost of the others activities, mainly feeding, that the male develops while he is away from the nest may be added to the cost associated with maintaining the heat of eggs. The portion of time that the bird is in the nest is not constant: it increases as the incubation advances. Based on Bruning (1974), Fernández and Reboreda [2003], and Piera [1874 in Davis [1977]] observations, we assumed that at the beginning of the incubation the bird leaves the nest up to four times in a day for as much as of 1 hour (observed maximum length) and that during the last part of the incubation (from day 30 to hatching) he remains all the day on the nest. We formulated the portion of the day that the bird is on the nest by

$$f\left(d\right)=\begin{cases}\frac{0.575.\mathrm{d}+82.75}{100} & if\ d<30\\ 1 & if\ \ d\geq 30\end{cases}$$

where d is the day of incubation.

Assuming that during the incubation the male leaves the nest only for feeding, the portion of the day when he feeds is given by: $1-f(d)$. Then, the FMR for males incubating can be formulated by

$$FMR=t_f\,.\,c_f+RC=\left(1-f\left(d\right)\right).\,24.\,c_f+M$$

where t_f and c_f are the time spent in feeding and its cost, respectively and RC is the cost associated with incubation.

The value of M was obtained daily considering that the average male incubates 26 eggs whose mean weight is 647 g (Fernández and Reboreda [1998]). The proportion of the egg's surface covered by the bird during incubation was assumed to be 0.4, the specific heat of the egg is 0.78 cal/g °C, the temperature of the eggs incubating was 35 °C, temperature of the nest 20 °C, and cooling rate of the eggs 0.47 °C/°C hour (GJF, unpubl. data). The portion of the day that the male is on the nest changes daily, as was mentioned above.

Thus, the reproductive energetic cost is added to the other accumulated energetic costs,—differentiating between males and females—, for obtaining the yearly accumulated energetic cost for individuals that engage in reproduction. Note that while the reproductive female continues engaging into the usual pattern of activities, the incubating male's only activities are resting over the nest and spending short periods in the vicinity of the nest for feeding. The average daily energetic cost for reproductive individuals can be estimated by dividing this by 365 days.

Since the purpose of this work is to estimate energetic costs and not to calculate an energy balance, it is not necessary to daily update the individuals' weight. However, it is reasonable to update weights at the beginning of each season.

It is assumed that individuals intend to reproduce and thus choose a strategy that will allow them to gain weight, but not to decrease it. At the beginning of the postreproductive season, the simulation assigns each individual a weight in the range from 21 to 30 kg. At the end of the postreproductive season and beginning of the nonreproductive, another weight is drawn at random and compared to the previous one. If the new weight is higher, it is assigned to the individual, but if it is lower, the individual maintains its weight. The procedure is repeated at the end of this season and beginning of the reproductive season.

Simulations. With the aim of analyzing the sensitivity of the model and defining whether FMR is different in individuals that reproduce successfully from those which do not reproduce, we ran a set of simulations considering different possible situations. Each simulation estimated the energetic cost for 500 individuals and 10 simulations were performed for each combination of parameters. The amount of simulations necessary to cover all different combinations of parameters was 54 for females and 18 for males. The number of combinations for females was larger than that for males because the breeding costs involved are associated with a larger set of parameters. Distribution of time dedicated to each activity was assigned daily to each individual randomly from a set of field observations for each season (postreproductive, nonreproductive, and reproductive). In each simulation, we considered a speed of displacement associated with foraging and a different one associated with locomotion. Naturally, the costs associated with foraging as well as to locomotion depend on the speed of displacement. Three speeds of displacement during foraging (0.5, 1 and 1.5 km/h) and three speeds of displacement for locomotion (2, 2.5 and 3 km/h) were taken into account.

We considered two alternatives for assigning the amount of eggs that one female lays: either a fixed amount of eggs or an amount associated with her breeding season's weight. In the second case, we assumed that when the weight is bellow 23 kg she may lay less than eight eggs; if the weight is between 23 and 25 kg she may lay between 8 and 16 eggs; and if her weight is above 25 kg she may lay between 16 and 24 eggs. When the amount of eggs laid is fixed throughout one simulation, we considered that every female can lay either 0, 6, 12, 18 or 24 eggs during the breeding season.

For males, the simulations involved a fixed clutch of 26 eggs which was incubated during 38 days.

Given that the simulation outputs could be fitted by linear regression, we compared the slopes of these regressions using an ANOVA (Zar [1984]).

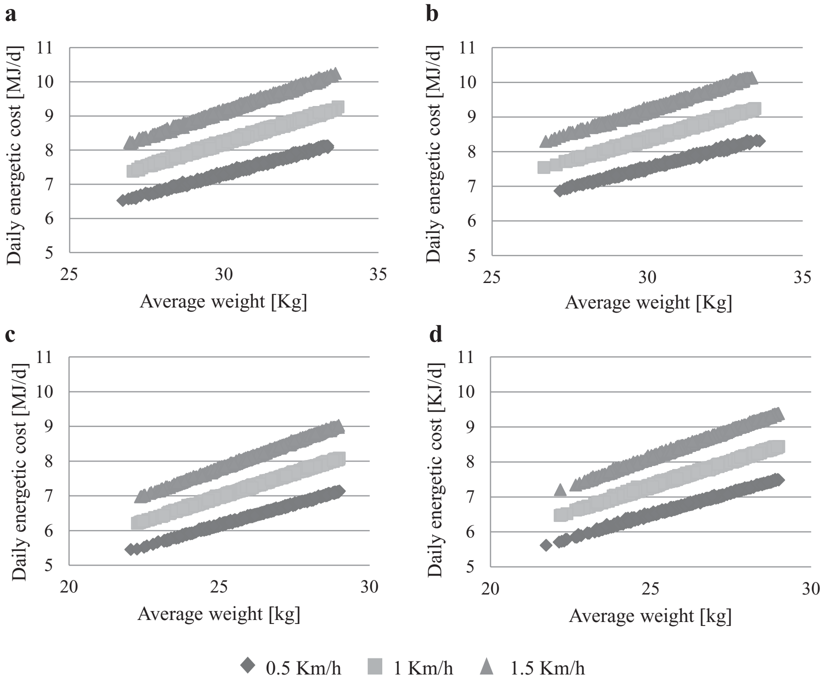

FIGURE 2. Daily energetic costs considering different speeds of displacement when foraging (◆ 0.5 km/h, ■ 1 km/h, ▲1.5 km/h) and a speed of 2 km/h for locomotion. (a) non breeding males, (b) breeding males, (c) females that do not lay eggs, and (d) females that lay 24 eggs in a season.

3. Results. The calculated individual daily energetic costs, in terms of FMR, are statistically different when either the speed at foraging or the speed of locomotion is modified, all the other parameters remaining fixed ($p < 0.05$).

The outputs were most sensitive to the speed at foraging, that is, in all cases (breeding males, nonbreeding males, as well as females) changes in the speed at foraging produced the larger changes in the value of the FMR (Figure 2). The output exhibited variations also when a change in the speed of locomotion was introduced while all other parameters remained fixed. However, their magnitudes were smaller than in the previous case (Figure 3). The slopes of the linear regressions fitting the costs depending on individual weight increases vary for different foraging and locomotion speeds in all cases (Table 3 and Table 4). Note that the slopes increase as displacement speeds increase, so that the costs increase is much more important for heavier individuals (males or females) than for younger ones.

We observed that when the speed at foraging was 0.5 km/h, maximum and minimum daily energetic costs estimated here were between the rate given by Nagy

TABLE 3. Slopes of the linear regressions fitting the costs vary as individual's weight increases, for breeding and non breeding adult males considering different foraging and locomotion speeds.

Speed when foraging [km/h]	Speed when moving [km/h]	Slope of linear regression fitting costs for successful breeding males [MJ/d]	Slope of linear regression fitting costs for non breeding males [MJ/d]
0.5	2	0.225	0.241
	2.5	0.229	0.248
	3	0.234	0.253
1	2	0.252	0.272
	2.5	0.255	0.276
	3	0.260	0.281
1.5	2	0.277	0.300
	2.5	0.282	0.307
	3	0.287	0.312

TABLE 4. Slopes of the linear regressions fitting daily costs as individual's weight increases, for breeding (maximum number of eggs) and non breeding females considering different foraging and locomotion speeds.

Speed when foraging [km/h]	Speed when moving [km/h]	Slope of linear regression fitting costs for breeding females 24 eggs [MJ/d]	Slope of linear regression for non breeding females non breeding females [MJ/d]
0.5	2	0.255	0.244
	2.5	0.260	0.250
	3	0.266	0.255
1	2	0.288	0.277
	2.5	0.293	0.283
	3	0.299	0.288
1.5	2	0.320	0.309
	2.5	0.325	0.316
	3	0.331	0.321

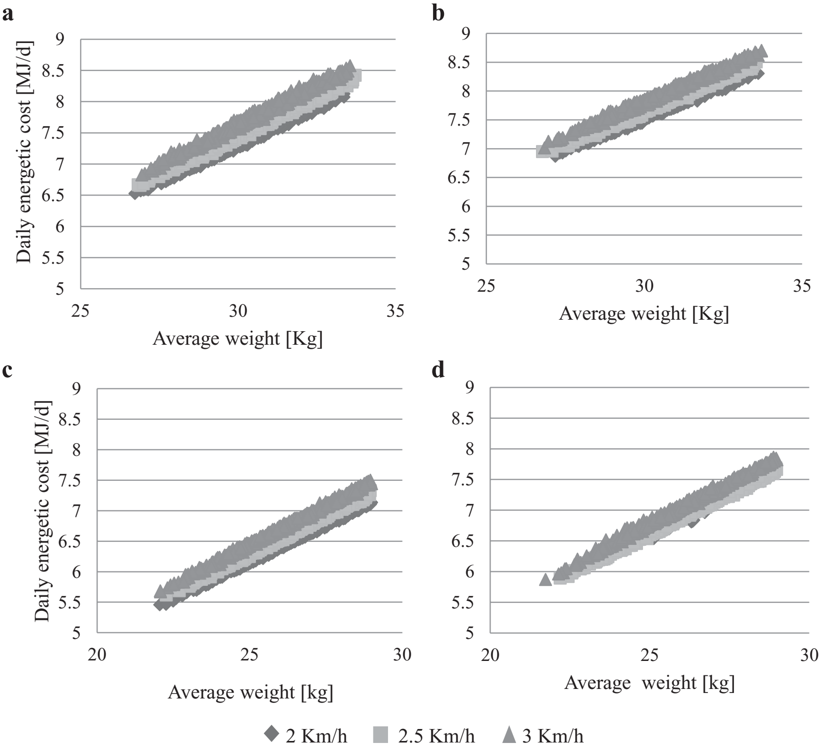

FIGURE 3. Daily energetic cost considering a speed of 0.5 km/h when foraging and different speeds of locomotion (◆ 2 km/h, ■ 2.5 km/h, ▲ 3 km/h): (a) nonbreeding males, (b) breeding males, (c) females that do not lay eggs, and (d) females that lay 24 eggs.

[2005] for omnivorous birds and the rate corrected by phylogeny given by Tieleman and Williams [2000] (Figure 4). These rates are higher than those estimated by Simoy (2011) when the 10-hour photoperiod is considered. When the speed of foraging was raised to 1 km/h, all daily energetic costs obtained were higher than those given for omnivorous birds. When the weights were lower than 30 kg the estimated costs were close to the rate corrected by phylogeny given by Tieleman and Williams [2000] but for heavier weights the costs were much higher (Figure 5). These rates are higher than those estimated by Simoy [2011] when the 15-hour photoperiod is considered. Finally, when the speed was 1.5 km/h, the estimated costs were higher than those given from the rate corrected by phylogeny (Tieleman and Williams [2000]) and much lower than the rates given for all birds.

Some examples of the magnitude of daily costs for males and females, comparing breeding and non breeding individuals can be seen in the Table 5 and Table 6. As

TABLE 5. Examples of daily metabolic costs for breeding and non breeding males considering different foraging and locomotion speeds.

Speed when foraging [km/h]	Speed when moving [km/h]	Costs for successfully breeding males [MJ/d] 30 kg	Costs for successfully breeding males [MJ/d] 35 kg	Costs for non breeding males [MJ/d] 30 kg	Costs for non breeding males [MJ/d] 35 kg
0.5	2	7.256	8.652	7.303	8.509
	2.5	7.668	8.815	7.466	8.705
	3	7.808	8.980	7.629	8.891
1	2	8.361	9.618	8.218	9.576
	2.5	8.503	9.780	8.380	9.762
	3	8.646	9.946	8.544	9.950
1.5	2	9.196	10.581	9.133	10.635
	2.5	9.340	10.752	9.294	10.828
	3	9.483	10.918	9.460	11.018

TABLE 6. Examples of daily metabolic costs for breeding (maximum number of eggs) and non breeding females considering different foraging and locomotion speeds.

Speed when foraging [km/h]	Speed when moving [km/h]	Costs for breeding females 24 eggs [MJ/d] 22 kg	Costs for breeding females 24 eggs [MJ/d] 25 kg	Costs for non breeding females [MJ/d] 22 kg	Costs for non breeding females [MJ/d] 25 kg
0.5	2	5.718	6.482	5.418	6.151
	2.5	5.847	6.627	5.548	6.298
	3	5.979	6.776	5.679	6.446
1	2	6.434	7.297	6.135	6.967
	2.5	6.565	7.444	6.264	7.113
	3	6.694	7.590	6.396	7.260
1.5	2	7.155	8.114	6.855	7.784
	2.5	7.287	8.262	6.982	7.929
	3	7.414	8.407	7.115	8.076

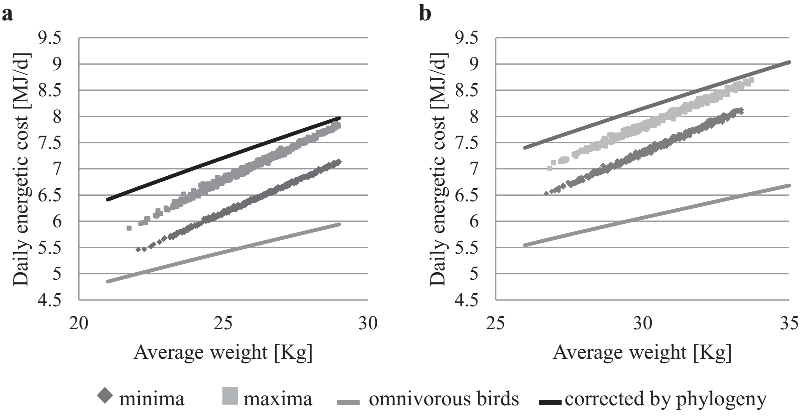

FIGURE 4. Maximum (■) and minimum (◆) daily energetic costs estimated for considering a speed of displacement of 0.5 km/h when foraging as compared to the rate given by Nagy (2005) for omnivorous birds (gray line) and the rate corrected by phylogeny (black line) given by Tieleman and Williams (2000): females (a) and males (b). The minima costs are associated with non breeding animals.

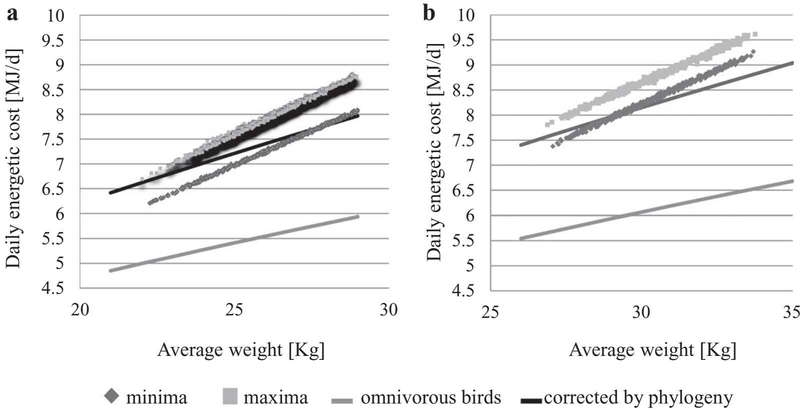

FIGURE 5. Maximum and minimum daily energetic cost estimated considering a speed of displacement of 1 km/h when foraging as compared to the rates given by Nagy (2005) for omnivorous birds (gray line) and the rate corrected by phylogeny (black line) given by Tieleman and Williams (2000): (a) females and (b) males. The minima costs are associated with non breeding animals.

expected, daily energetic costs, in terms of FMR, exhibit a statistically significant difference between individuals who breed (males and females) and those who do not breed, when all other parameters are being fixed ($p < 0.05$). For females in particular, a significant difference was observed as the amount of eggs laid varies

($p < 0.05$). When the amount of eggs increases, all other variables being fixed, the daily energetic costs also increase, as expected. When the amount of eggs laid depends on the weight of the female, a greater variability in the estimated daily energetic cost can be observed. Also, the costs for non breeding males may be higher than for breeding males when the individual is heavy and moves faster or when the individual is thin and moves slowly (Tables 5 and 6). Observe that a lighter male that moves slowly can accumulate a higher cost that the same animal at rest, and also a heavier male moving at a high speed can accumulate costs higher that the same animal at rest. Hence, this apparent anomaly points towards two aspects: (i) the numbers in Table 5 are annual averages computed over a spectrum of possible behaviors, and (ii) higher costs do not mean a lower energy balance for nonbreeding individuals because while moving they will be ingesting food, something that the breeding male at rest may not do. These results on costs show that for a clearer understanding of the low reproductive success in rheas it will be necessary to resort to energy balances.

4. Discussion.

Populations of Greater Rheas have declined in the last decades as a consequence of the high habitat transformation into crop fields, resulting in animals been chased from their territories, and also because poaching. Habitat transformation does not directly impact food availability but rather makes difficult finding grounds that area appropriate for nesting and for establishing a population even if it is small. At present, it is considered a "near threatened" species according to the IUCN [2012], because of its declining population trend. Since the growth of a population depends mostly on the breeding success of its individuals, understanding the factors affecting this success becomes a priority in view of the conservation of a species.

As mentioned earlier, the purpose of this work is to estimate daily energetic costs taking into account the individual's behavior depending on the season and distinguishing between sexes and also between reproductive and non reproductive animals and not to calculate an energy balance.

An interesting aspect of this type of models is that the resulting FMR is not equal for all the individuals of a given weight; it varies depending strongly on the behavior. This allows modeling each individual as a function of its individual characteristics and not only based on the corporal weight as the allometric equations do. In this way, a restless individual will have a greater FMR than a sedentary individual, even if they have the same weight.

The model proposed here was constructed using the costs of some activities reported in the literature. All daily energetic cost here estimated fall within the confidence interval given by Nagy [2005] for omnivorous birds.

The differences between these rates and the rates estimated by Simoy [2011] are, on the one hand, because here we estimate the daily cost as an annual average modifying the individual's weight seasonally, while the previous work estimated the cost for only one given day. On the other hand, in this work the night rest cost is considered as RMR while Simoy [2011] considered it as BMR disregarding thermoregulation cost.

The costs associated with displacement depend on speed, which is certainly different among individuals. Once the speed range is determined, either for foraging or for locomotion, it is possible to analyze the sensitivity of the model relative to these parameters. The model exhibits a higher sensitivity to variations in the speed of foraging than in the speed of locomotion, as seen by percentage output versus percentage input. When analyzing variations in both parameters, it is easily seen that the speed at foraging has a larger impact on energy costs than the speed of locomotion. This does not necessarily relate to the formulation of the cost of the activity but rather to the time that the individuals dedicate to these activities.

The model showed statistically significant differences between individuals which breed and those which do not breed. It is not surprising that in almost every case nonreproductive individuals exhibited lower costs than the reproductive ones. Nevertheless, the model does not allow to determine whether the energetic costs associated with the breeding are the reason why few individuals try to reproduce but it indicates that there is a clear difference in the daily energetic costs of individuals which reproduce and those which do not reproduce.

In the simulations, each day the birds are randomly assigned a behavior from a set of observed patterns. The minimal and maximal daily energetic costs are estimated by choosing for each season the field observation that yields the minimum and maximum results respectively. It is possible to observe that successful breeding individuals are capable of exhibiting lower daily costs than non breeding individuals if they choose the adequate behavioral patterns. This makes clear how important is individual behavior for reaching adequate fitness level, in terms of accumulated energy, before attempting reproduction. We have not considered the parental care cost. However, it is clear that it would only increase the daily cost and thus widen the difference between males that reproduce successfully and males that do not reproduce.

As an example, we can take a 30-kg male that reproduces successfully. His daily activities may generate an energetic cost as low as 6805 kJ/d if he chooses in each season a pattern that produces the minimal cost, as high as 8611 kJ/d if he chooses a pattern that produces the maximal cost, or 7526 kJ/d if his pattern is random among those observed during each season. For a 30 kg male that does not reproduce the costs when choosing the minimal, the maximal or the random pattern are 6430 kJ/d, 8500 kJ/d y 7303 kJ/d, respectively. In all cases, the foraging and displacement speeds were kept at 0.5 km/h and 2 km/h, respectively. It is worth noting that breeding individuals barely feed while nesting (lower cost but no energy uptake) but not breeding move around for foraging and thus increase their FMR (energy intake but higher cost).

In the case of males, the most costly behavior is that which in the post reproductive season allows 52% of the day to foraging, 45% to displacements, and 3% to preening, aggression and vigilance; during the non reproductive season 50% to foraging, 48% to displacements and 2% to preening, aggression and vigilance, while 58% of the day is devoted to foraging, 35% to displacements, and 7% to preening, aggression and vigilance during the reproductive season.

On the other hand, the least costly behavior is that which is composed of the following distribution: in the post reproductive season 69% of the day to foraging, 1% to displacements, and 30% to preening, aggression and vigilance; during the non reproductive season 38.5% to foraging, 11% to displacements and 50.5% to preening, aggression and vigilance, while during the reproductive season 12% of the day is devoted to foraging, 2% to displacements, 4% to preening, aggression and vigilance, and 81% to resting. In all cases, the time corresponding to portion of the day relates to the photoperiod, which explains the differences among seasons. The time assigned to nocturnal rest is the difference between 24 hours and the length of the photoperiod. It is clear that the birds could select behavioral patterns that are less costly for reducing the energetic costs during the non reproductive season and accumulating the necessary energy for successfully reproducing.

Although the differences in the costs are significant, their magnitude is not really large from the point of view of energy (see Tables 5 and 6). This may relate to the form in which the daily costs were calculated. Here we fixed each individual's weight over one season and updated it when a new season began. Another possibility would be to calculate the energy costs every day and to immediately update the weight. This requires performing a daily energy balance. However, this would mean a totally different approach that requires knowing how much food the bird consumes, depending on weight, sex and season, and the food's energetic value, not to mention the individual's metabolism.

Also, it is important to note that the differences between breeding and non breeding males could have been larger if the posthatching costs had been included in the calculations. Rheas are precocial birds but nevertheless exhibit uniparental male care. Males take care of the chicks for 4–6 months. They allocate less time to feeding and more time to vigilance and walking than males in groups of adults or solitary males. Their investment in vigilance decreases as the chicks aged (Fernández and Reboreda [2003]). We did not include these costs in our estimations because of the lack of sufficient field data on how the males allocate their time to these activities during the posthatching period.

Since the allocation of time to feeding during incubation and posthatching is reduced to almost none, once the incubation period is over, the male still needs its energy reserves for completing a successful reproduction. Hence, breeding males need to recover their corporal weight before attempting to accumulate the reserves that may allow them to initiate a new reproductive period. Thus it seems reasonable to think that a minimal body weight is required that may allow a male individual to complete the full reproductive season without risking his health and without abandoning his nest or his offspring.

5. Conclusions.

The model was constructed with the purpose of estimating the individual energetic cost by taking into account the individual's behavioral pattern in the postreproductive, nonreproductive, and reproductive seasons as well as the individual's corporal weight, the sex and differencing between reproductive and non reproductive individuals.

One interesting aspect of this model is that the differences in behavior are reflected in the resulting FMR even though the individuals had the same weight. This allows modeling each individual as a function of its individual characteristics and not only based on the corporal weight as allometric equations do.

The model allows inferring which patterns of behavior are more advantageous to the individual. We feel that this is an important step forward because it allows characterization of individuals in an efficiency scale. The model can be used to analyze different behavioral patterns identified in particular individuals or groups in real populations and can be used as a tool to understand why some groups of rhea have low reproductive success, although it cannot offer a definite and quantitative answer. Also it can help analyze how environmental changes may influence the population dynamics. For example, in the future climate changes may reduce food availability and force populations to larger displacements for foraging, thus affecting individual costs and ultimately the recruitment.

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ethical requirements for scientific research of the University of Buenos Aires and comply with the current laws of Argentina.

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