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LOW COSTS OF TERRESTRIAL LOCOMOTION IN WADERS

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Energy expenditure of terrestrial locomotion on a linear treadmill was measured in five wader species: Turnstone *Arenaria interpres*, Knot *Calidris canutus*, Grey Plover *Pluvialis squatarola*, Oystercatcher *Haematopus ostralegus* and Bar-tailed Godwit *Limosa lapponica*. Additional data on Redshank *Tringa totanus* were taken from the literature. The cost of running in these waders, measured as the slope of the regression line of energy expenditure against speed of locomotion, is significantly less than an allometrically calculated slope for all bird species (Taylor *et al.* 1982). It is also less than in grouse species which, like waders, must walk to gather their food. Cost of running for a 100 g wader is 22% below the cost of a grouse, and 68% below the cost of a hypothetical penguin of similar mass. Intra-individual cost of running in relation to body mass of a Turnstone and inter-individual cost of running in Knots reveal much stronger increases of running costs with increasing body mass than interspecific allometric relations would predict, and this elevated activity cost probably importantly influences the set point for body mass regulation in birds.

Key words: *Calidris canutus* - *Arenaria interpres* - energetics - cost of foraging - walking - treadmill - allometric scaling - body mass regulation

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INTRODUCTION

Many birds spend a major part of the day walking in search for food; costs of terrestrial locomotion (or costs of running) must loom large in the energy budget of these birds. A precise determination of the cost of running of a species might provide us with better estimates of the costs of foraging, thereby adding a building block to our understanding of habitat use, migration strategies and reproductive decisions. Our study on the cost of running in waders is part of a larger research programme focussed on the ecological energetics of waders, in particular of Red Knots *Calidris canutus* (Piersma 1994). Previous studies on wader energy expenditure paid attention to levels of resting metabolic rate in temperate regions (Kersten

& Piersma 1987), tropical areas (Piersma *et al.* 1995; Kersten *et al.* 1998), cost of thermoregulation in relation to weather variables (Wiersma & Piersma 1994) and the interaction between thermoregulation and activity costs (Bruinzeel & Piersma 1998). Foraging costs were only measured in caged birds (Poot and Piersma 1994). Field estimates are still lacking. For the modelling of total energy expenditure, the next challenging task will be the quantification of the activity (foraging) costs in the field. As a first step towards this approach we have analysed the cost of running in waders, and as a second step we have considered the effects of mass increase upon this cost. In contrast to the costs of flying and swimming, the cost of running is a linear function of speed (Taylor *et al.* 1970). Cost of running is usually

analysed by estimating the slope of the regression line of energy expenditure (in $J s^{-1}$) on running speed (in $m s^{-1}$) (Fedak *et al.* 1974). The slope of this relation provides an estimate of the energy expenditure per unit distance travelled (in $J m^{-1}$). We refer to this cost per unit distance travelled as 'cost of terrestrial locomotion' or 'cost of running'. The unit makes it possible to scale the economics of running on body mass for different individuals, species, or groups of species.

MATERIALS AND METHODS

All waders were caught with mist nets in the Dutch Wadden Sea (53°28'N, 06°10' E) and were then kept in outdoor cages of 2 by 4 by 2m in Groningen (53°11'N, 06°36'E). The birds were fed *ad libitum* with commercially available trout-food pellets (Trouvit) consisting of 11% water, 12% fibres, 3% cellulose, 45% protein and 8% fat; or a similar product (Pelsifood: 7% water, 38.2% protein, 17.8% fat, 22.0% carbohydrates).

The birds were trained to walk on a linear treadmill consisting of a continuous running belt with a surface of rough rubber. On a linear treadmill one measures locomotion in a straight line, while the bird is remaining at a fixed position in the metabolic chamber. This differs from a circular treadmill where the bird runs in circles and moves through the metabolic chamber. On the treadmill birds walked without slipping or falling. The experimental conditions for Knots differed from those of the other waders. The treadmill was driven by an electro-engine and placed in an airtight aluminium chamber of about 12 L (Knots) or 48 L (other species). Steady state oxygen consumption was considered to be reached within 25 min (Knots) or after 45 min (other species). For a detailed description of the measurements on Knots, see Bruinzeel & Piersma (1998). Oxygen consumption was measured with an open flow respirometer, using Applied Electrochemistry S-3A and S-3A/II oxygen analysers (accuracy 0.002%). Exhaled air was dried using a 3Å molecular filter and some silicagel. Energy expenditure

was calculated after Hill (1972), assuming a respiration quotient of 0.73 and a corresponding energy equivalent of 20 $kJ L^{-1} O_2$ (cf. Wiersma & Piersma 1994). All birds were measured under thermoneutral conditions (25°C for Knots and Turnstones, above 20°C for the larger waders) and in post-absorptive state i.e. starved for 24 h (Knots) or at least for 6 h (other species) (see Piersma *et al.* 1995). The birds were weighed before and after the running experiment. In the following analyses average body mass was used.

Running costs (in $J m^{-1}$) were calculated as the slope of the regression line of energy expenditure ($J s^{-1}$) on running speed ($m s^{-1}$), including data points collected at zero speeds to allow comparison with results of others. Nevertheless, we excluded data points gathered at very low speeds, since at these speeds birds were walking in short bouts rather than showing a continuous gait. Walking in short bouts leads to higher costs due to costly accelerations.

Values for other species were gleaned from the literature and converted into Watts, kg and $m s^{-1}$ for consistency; all data were logarithmically transformed prior to statistical analysis. A data point originating from a Wilson's Plover *Charadrius wilsonia* reported in Taylor *et al.* (1982) that originated from a personal communication mentioned in Fedak & Seeherman (1979), appears aberrant. The reported body mass of 18 g is unrealistic as Wilson's Plovers normally weigh 55 g. Because we could not trace the original data, we kept this species out of the statistics. Two studies on Quail *Coturnix coturnix* (Nomoto *et al.* 1983 and Warncke *et al.* 1988) report different costs of running, in spite of having worked with birds of nearly identical body mass. We therefore used the average of the values reported by the two studies in the statistical analysis. In addition, we restricted our review to birds with a similar gait. Birds that hop instead of step (e.g. sparrows) were not included in our review, as this mode of locomotion is so different from the normal running gait of waders (for instance, storage of energy might occur between hops; see Bennett & Taylor 1995).

RESULTS

Cost of running in waders

In Table 1 we summarise our measurements of the costs of running in waders. The cost of running is significantly lower than the predictions based on the allometric relation for all birds ($10.7 M^{0.684}$) derived by Taylor *et al.* (1982) (Wilcoxon matched pairs signed rank test $P < 0.05$, $n = 6$). On average, waders run at an energetic cost which is 32% (range 27–37%) below the predicted value.

All available studies on running costs in birds (Table 2) are presented in Fig. 1 as a function of body mass. The data are grouped into five eco-morphological groups: penguins, geese, grouse, waders and others. The allometric relations describing cost of running (in $J m^{-1}$) as a function of body mass (M in kg) in the different groups are:

penguins	$22.5 M^{0.68}$ ($R^2 = 1.00$, $n = 5$, $P < 0.001$)
grouse	$10.9 M^{0.75}$ ($R^2 = 0.99$, $n = 7$, $P < 0.001$)
waders	$7.8 M^{0.72}$ ($R^2 = 0.98$, $n = 6$, $P < 0.001$)

The allometric regression coefficient for the geese ($n = 3$) was not significantly different from zero. Cost of running for waders was significantly lower than that for grouse (ANCOVA, $F = 784$, $df = 2$, $P < 0.001$) and much lower than that for penguins (ANCOVA, $F = 6214$, $df = 2$, $P < 0.001$). Cost of running for a 100 g wader is 22% below the cost of a similar sized grouse, and 68% below the cost of a (hypothetical) penguin of similar mass.

Mass-related variation in running costs

To study the effects of changes in mass on the cost of locomotion within a species, experimental animals must be supplied with artificial weights or themselves show mass variation. In this study we used natural variation in body mass among different individual Knots, and the natural seasonal variation within one individual Turnstone, to estimate intraspecific locomotion costs (Fig. 2). Cost of running ($J m^{-1}$) as a function of body mass (kg) for Knots is described by the relation: cost of running = $840 M^{2.90}$ ($n = 9$, $R^2 = 0.60$).

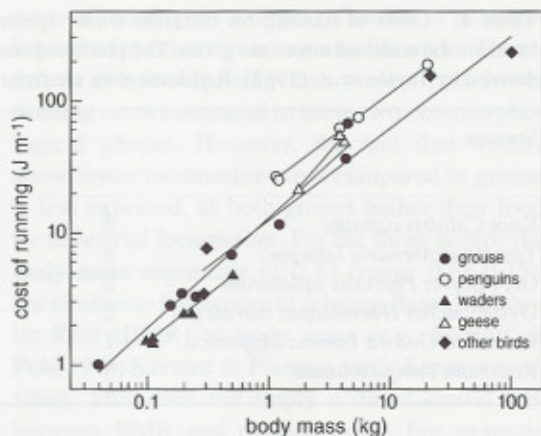


Fig. 1. Double-logarithmic plot of interspecific cost of terrestrial locomotion. Cost of running ($J m^{-1}$) as a function of body mass (kg). The data are presented in Table 2. The lines represent allometric relations for the three eco-morphological groups (see text).

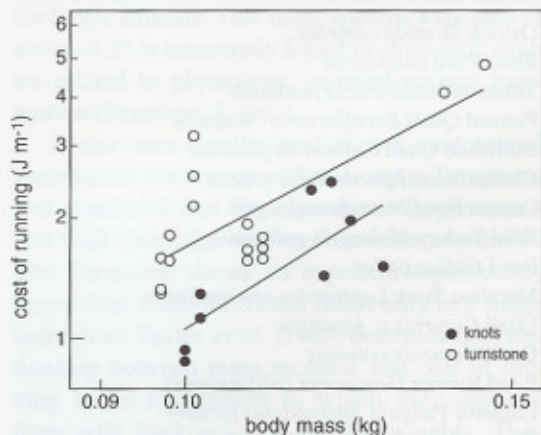


Fig. 2. Intra-specific cost of running for Knots (closed dots) and intra-individual variation in running costs of one Turnstone (open dots). Cost of running ($J m^{-1}$) is plotted as a function of body mass (kg).

For the Turnstone the cost of running as a function of body mass is described by the relation: cost of running = $337 M^{2.28}$ ($n = 16$, $R^2 = 0.55$). The values of 2.28 (95% confidence interval 1.07–3.39)

Table 1. Costs of running for different wader species, *n* gives the number of individuals tested and between brackets the standard errors are given. The predicted cost of running is based on the allometric relation ($10.7 M^{0.68}$) derived by Taylor *et al.* (1982). Redshank data are from Speakman (1984).

Species	<i>n</i>	Body mass (kg)	Cost of running (J m ⁻¹)	Predicted cost of running (J m ⁻¹)
Knot <i>Calidris canutus</i>	5	0.109 (0.005)	1.48 (0.26)	2.35
Turnstone <i>Arenaria interpres</i>	8	0.110 (0.004)	1.58 (0.13)	2.36
Grey plover <i>Pluvialis squatarola</i>	2	0.205 (0.04)	2.54 (0.14)	3.62
Oystercatcher <i>Haematopus ostralegus</i>	2	0.501 (0.04)	4.85 (0.03)	6.67
Bar-tailed Godwit <i>Limosa lapponica</i>	1	0.228	2.51	3.89
Redshank <i>Tringa totanus</i>	>15	0.095	1.52	2.14

Table 2. Species, body mass (kg) and cost of running (J m⁻¹). Data from the literature are combined with new data. Authorities: ¹Fedak & Seeherman (1979); ²Taylor *et al.* (1971); ³Taylor *et al.* (1982); ⁴Brackenburry & Avery (1980); ⁵Bamford & Maloij (1980); ⁶Nomoto *et al.* (1983); ⁷Warncke *et al.* (1988); ⁸Pinshow *et al.* (1977); ⁹Bevan *et al.* (1995); ¹⁰Baudinette & Gill (1985); ¹¹Funk *et al.* (1989); ¹²Nolet *et al.* (1992); ¹³This study; ¹⁴Speakman (1984).

Species	Body mass (kg)	Cost of running (J m ⁻¹)	Authority
Ostrich <i>Struthio camelus</i>	103	226.6	1
Rhea <i>Rhea americana</i>	22.0	149.6	2
Tinamou <i>Nothoprocta pentlandi</i>	0.31	7.44	3
Painted Quail <i>Excalfactoria chinensis</i>	0.04	1.01	3
Bobwhite Quail <i>Colinus virginianus</i>	0.19	3.42	3
Chukar Partridge <i>Alectoris graeca</i>	0.49	6.762	3
Guinea Fowl <i>Numida meleagris</i>	1.21	11.37	3
Wild Turkey <i>Meleagris gallopavo</i>	4.31	35.34	3
Fowl <i>Gallus gallus</i>	0.25	3.274	4
Marabou Stork <i>Leptoptilos crumeniferus</i>	4.50	64.8	5
Quail <i>Coturnix c. japonica</i>	0.16	4.19	6
Quail <i>Coturnix coturnix</i>	0.15	1.36	7
Road Runner <i>Geococcyx californianus</i>	0.29	3.422	1
Emperor Penguin <i>Aptenodytes forsteri</i>	20.8	178.9	8
Gentoo Penguin <i>Pygoscelis papua</i>	5.59	71.21	9
Adelie Penguin <i>Pygoscelis adeliae</i>	3.89	59.13	8
Little Penguin <i>Eudyptula minor</i>	1.2	24.39	10
White-flipped Penguin <i>Eudyptula albosignata</i>	1.15	25.53	8
Greylag Goose <i>Anser anser</i>	3.81	54.86	3
Canada Goose <i>Branta canadensis</i>	4.20	47.88	11
Barnacle Goose <i>Branta leucopsis</i>	1.78	21.20	12
Knot <i>Calidris canutus</i>	0.109	1.48	13
Turnstone <i>Arenaria interpres</i>	0.110	1.58	13
Grey Plover <i>Pluvialis squatarola</i>	0.205	2.54	13
Oystercatcher <i>Haematopus ostralegus</i>	0.501	4.85	13
Bar-tailed Godwit <i>Limosa lapponica</i>	0.228	2.51	13
Redshank <i>Tringa totanus</i>	0.095	1.52	14

for the exponent in the Turnstone, and the value of 2.90 (95% confidence interval 0.88-3.78) for the exponent in Knots, in spite of wide error margins, are clearly larger than the value of 0.68 given by Taylor *et al.* (1982) for all birds and higher than the inter-specific exponent of 0.72 for all wader species.

DISCUSSION

It has been shown before that cost of running in birds is a function of body mass (Taylor *et al.* 1970), but here we demonstrate that this relationship differs between eco-morphological groups. Although we quantified running costs from the slope of the relationship between speed and energy expenditure, this approach does not lead to a full quantification. This is because the impact of locomotion does not only lead to an increase in energy expenditure in relation to speed, but also leads to an increase in energy expenditure while not actually running, i.e. at the intercept. This cost at zero speed is a cost for maintaining posture. A high cost involved in maintaining the posture may depress the slope, while in reality the costs of running are unchanged. However, inclusion of intercept costs in the estimation of running cost will lead to speed-dependent estimates. Given the large differences in locomotion speeds between birds species (depending on foraging methods and prey, see for instance Speakman & Bryant 1993), these would yield unsatisfying comparisons.

The relatively high costs of terrestrial locomotion in penguins and geese have already been known for twenty years (Pinshow *et al.* 1977). During running both orders show a gait with a strong lateral displacement (also called 'waddling'), which is a costly process because the energy is not only invested in the main direction but also in sideways displacement. This is illustrated by the gait of Emperor Penguins *Aptenodytes forsteri* in which the tail leaves a sinusoidal track in the snow during their terrestrial migration (Pinshow *et al.* 1977). Penguins and geese are well adapted to aquatic environments and their high

costs of running are a direct reflection of morphological adaptations to an aquatic life-style. Therefore it is not surprising that waders face lower running costs compared to these two eco-morphological groups. However, the fact that waders show lower locomotion costs compared to grouse is less expected, as both groups gather their food by terrestrial locomotion. For the three groups the body mass exponents of 0.73 (range 0.68-0.75), are similar to the exponent relating Basal Metabolic Rate (BMR) to body mass (*e.g.* Aschoff & Pohl 1970; Kersten & Piersma 1987; Kersten *et al.* 1998). This does not imply a direct causal link between BMR and running costs. For example waders have low running costs, but have relatively high BMR's (Kersten & Piersma 1987). It is striking that a similar mass exponent (0.72) is also found for the cost of diving in birds (De Leeuw 1996). On a mass-specific basis, cost of running scales proportional to $M^{-0.25}$ to $M^{-0.32}$, so the cost of moving one kg of body mass is much cheaper for larger animals. This mass-specific exponent of about -0.25 is commonly found in allometric studies related to physiology, metabolism and locomotion (Pennycuik 1992).

In our intra-specific analysis we used natural variation in body mass of Knots and a Turnstone, and concluded that the exponent is larger than 1 and well above the interspecific mass exponents. The Turnstone shows an exponent significantly larger than 1, but this result refers only to a single individual. Taylor *et al.* (1980) determined a relationship between mass increase and cost of running in an experiment in which they supplied dogs with backpacks of various weights. They found that a relative mass increase was paralleled by an identical relative increase in the cost of locomotion, i.e. an exponent of 1. Assuming that intraspecific locomotion costs scale with an exponent of one, it is possible to derive an equation which predicts locomotion costs for all birds with different masses, by substituting the average mass of a species in the suitable allometric equation, and multiplying this result with the relative mass increase (current mass/average mass). Our calculated exponent for Knots may be a minimal esti-

mate. Heavy Knots weighing 180-220 g that were ready for take-off on long distance flights simply refused to walk on the treadmill, indicating a high cost of running. As these birds were twice as heavy during the rest of the experiments, they would have incurred at least a doubling of their locomotion costs.

The cost of running in waders is low compared with that of other birds. This might be an artefact caused by a high number of relatively expensive runners in our dataset, but more likely reflects the advantage of having relatively long legs. Longer legs might allow birds to cover a certain distance in fewer steps. Cost reduction due to long legs may also explain why the legs of wader chicks are already so well developed at hatching (Beintema & Visser 1989). The alternative explanation that wader chicks have long legs to escape predation seems invalid as hatchlings initially rely completely on mimicry (pers. obs.). It would be interesting to see how foraging costs develop in relation to the size of the legs and total body mass.

Lima (1986) argued that the set points for body mass are functionally influenced by predation risk and the unpredictability of feeding conditions. Mass-dependent foraging costs (or activity costs in general) can also be an important proximate factor for the regulation of body mass. Rapid body mass increase in migratory waders may also be explained as an adaptation to shorten the period of costly foraging as much as possible. A challenging task for future research would be to test if mass-dependent costs of activity are a major determinant in the functional regulation of body mass.

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SAMENVATTING

De energetische kosten van lopen bij steltlopers werden geschat door middel van metingen aan het zuurstofverbruik op een lopende band. Het energieverbruik tijdens lopen vertoont een lineair verband met de loopsnelheid. De hellingshoek van de relatie tussen energieverbruik ($J s^{-1}$) en loopsnelheid ($m s^{-1}$) is een schatter voor de loopkosten ($J m^{-1}$). Wij onderzochten vijf steltloper-soorten (Kanoetstrandloper *Calidris canutus*, Steenloper *Arenaria interpres*, Zilverplevier *Pluvialis squatarola*, Scholekster *Haematopus ostralegus* en Rosse Grutto *Limosa lapponica*) en vonden een waarde van de Tureluur *Tringa totanus* in de literatuur. Alle bleken lagere loopkosten te ondervinden dan andere vogels. In vergelijking met de literatuur, lieten de nieuwe getallen zien dat loopkosten systematisch verschillen tussen vogelgroepen. De duurste lopers zijn de pinguïns, gevolgd door de ganzen. Het goedkoopst zijn de steltlopers, de hoenders zitten er tussenin. Steltlopers lopen 22% goedkoper dan hoenderachtigen en 68% goedkoper dan pinguïns. Binnen vogelsoorten nemen de loopkosten met toenemend gewicht sterker toe dan we op grond van de vergelijking tussen soorten zouden verwachten. Gegevens van Kanoetstrandlopers en een Steenloper suggereren dat relatieve toenames van het gewicht gepaard gaat met een evenredige toenames van de loopkosten. De sterke toename van de loopkosten (en foerageerkosten) bij toenemend gewicht kan een belangrijke factor zijn bij de optimalisatie van het lichaamsgewicht.

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