

in the female's return, is presumably an adaptation to the large but highly variable marine resources of the austral ocean.

Michel Gauthier-Clerc, Yvon Le Maho, Yannick Clerquin, Samuel Draut, Yves Handrich

Centre d'Écologie et Physiologie Énergétiques, Centre National de la Recherche Scientifique, 23 rue Becquerel, 67087 Strasbourg cedex 2, France, and Institut Français pour la Recherche et la Technologie Polaire, 29280 Plouzané, France
e-mail: yvon.lemaho@c-strasbourg.fr

- Weimerskirch, H., Stahl, J. C. & Jouventin, P. *Ibis* **134**, 107–117 (1992).
- Cherel, Y. & Ridoux, V. *Ibis* **134**, 118–127 (1992).
- Jouventin, P. *et al. Mar. Ecol. Prog. Ser.* **106**, 11–19 (1994).
- Foxton, P. *Disc. Rep.* **28**, 191–236 (1956).
- Hart, T. J. *Disc. Rep.* **21**, 261–356 (1942).
- Barrat, A. *Com. Nat. Fr. Rech. Ant.* **40**, 9–52 (1976).
- Barré, H. *J. Physiol. (Paris)* **74**, 555–561 (1978).
- Wilson, R. P. *J. Field Ornithol.* **55**, 109–112 (1984).

Biomechanics

Penguin waddling is not wasteful

Penguins use twice as much metabolic energy as other terrestrial animals of a similar mass to walk a given distance^{1,2}, which was thought to be because side-to-side waddling requires excessive work. Here we show that waddling actually conserves mechanical energy and suggest instead that walking is expensive for penguins because their short legs require them to generate muscular force rapidly.

Many animals reduce the muscular work of walking by exchanging the gravitational potential energy and kinetic energy of the centre of mass, like an inverted pendulum³. But penguins' waddling gait appears to involve large fluctuations in lateral kinetic energy and a poor exchange of mechanical energy¹. To test the idea that penguin walking is expensive because it requires more mechanical work to lift and accelerate their body than other animals of a similar mass, we used a force platform to measure the vertical, fore–aft and lateral ground-reaction forces of five walking emperor penguins (*Aptenodytes forsteri*). Forces were integrated to calculate the centre-of-mass velocities, displacements, and fluctuations in gravitational potential energy and kinetic energy⁴.

The fluctuations in lateral velocity were nearly three times those in the fore–aft direction. Lateral-velocity fluctuations occurred about zero, whereas the fore–aft velocity fluctuated about the average walking speed. Thus, kinetic energy fluctuates much less laterally than in the fore–aft direction. At moderate walking speeds of about 0.5 m s⁻¹, fluctuations in lateral kinetic energy accounted for about 30% of the total kinetic-energy fluctuations — a large value compared with other terrestrial vertebrates^{5,6}.

Penguins recovered up to 80% of the

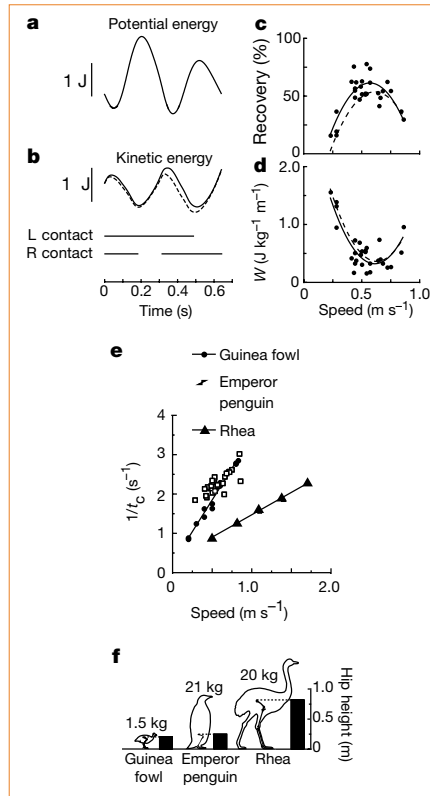


Figure 1 Biomechanics of penguin walking. **a,b**, Fluctuations in gravitational potential and kinetic energy of the centre of mass for an emperor penguin walking at 0.54 m s⁻¹. Bars, times when left or right foot was in contact with the ground. J, joules. **c,d**, Inverted pendulum recovery of mechanical energy (**c**) and work (*W*) per unit distance at a range of walking speeds (**d**). Dashed lines in **b–d** indicate the effect of excluding lateral kinetic energy from the analysis. **e**, Rate of generating muscular force, as indicated by the inverse of ground-contact time (1/*t_c*), for emperor penguin, guinea fowl (*Numida meleagris*)¹⁰ and rhea (*Rhea americana*) (P. G. Weyand, unpublished results), and **f**, standing hip height¹¹ (leg length). The metabolic costs of transport of emperor penguins (8.64 J kg⁻¹ m⁻¹) and guinea fowl (8.38 J kg⁻¹ m⁻¹) are twice those of rheas (4.23 J kg⁻¹ m⁻¹) (ref. 8).

mechanical energy during each stride, because of the similar amplitudes and out-of-phase fluctuations in gravitational potential and kinetic energies (Fig. 1a–c). This value is among the highest reported for any animal, indicating a large reduction in the mechanical work done by the penguin's muscular system (Fig. 1d). Recovery of mechanical energy was greatest and the work performed on the centre of mass per distance walked was least at about 0.5 m s⁻¹, a speed commonly used in nature².

Surprisingly, excluding lateral kinetic energy — that is, waddling — from our calculations would result in the recovery of less mechanical energy and more work being required from the muscles (Fig. 1b–d). Lateral movements increase the kinetic energy available to convert into gravitational potential energy and also cause these energies to fluctuate more completely out of phase.

Other components of work, such as rotating the body about the centre of mass

and swinging the limbs, probably do not account for the high cost: rotational work is approximately 10% of the total centre-of-mass work, and penguins have comparatively light, short limbs which offset their quick strides. At their preferred speed, emperor penguins perform the same amount of mechanical work to lift and accelerate their centre of mass as other walking animals of the same mass. Waddling therefore does not explain the high metabolic cost of penguin walking.

We propose instead that this high cost is due to rapid force generation. Regardless of the work muscles perform, they must actively generate force to support body-weight, and this cost is proportional to the magnitude and rate of generating force^{7,8}. At the same walking speed, emperor penguins and rheas — a flightless bird of a similar mass — generate the same average force on the ground. But because of their comparatively short legs, emperors generate this force twice as fast (Fig. 1e, f), requiring faster, less economical muscle fibres⁹. Our results indicate that it is their short legs, and not their waddling gait, that accounts for the high cost of penguin walking.

Timothy M. Griffin*, Rodger Kram†

*Integrative Biology Department, University of California, Berkeley, California 94720-3140, USA

†Department of Kinesiology and Applied Physiology, Campus Box 354, University of Colorado, Boulder, Colorado 80309-0354, USA
e-mail: tmgriff@uclink4.berkeley.edu

- Pinshow, B., Fedak, M. A. & Schmidt-Nielsen, K. *Science* **195**, 592–594 (1977).
- Dewasmes, G., Le Maho, Y., Cornet, A. & Groscolas, R. *J. Appl. Physiol.* **49**, 888–896 (1980).
- Cavagna, G. A., Heglund, N. C. & Taylor, C. R. *Am. J. Physiol.* **233**, R243–R261 (1977).
- Cavagna, G. A. *J. Appl. Physiol.* **39**, 174–179 (1975).
- Farley, C. T. & Ko, T. C. *J. Exp. Biol.* **200**, 2177–2188 (1997).
- Cavagna, G. A., Saibene, F. P. & Margaria, R. *J. Appl. Physiol.* **18**, 1–9 (1963).
- Kram, R. & Taylor, C. R. *Nature* **346**, 265–267 (1990).
- Roberts, T. J., Kram, R., Weyand, P. G. & Taylor, C. R. *J. Exp. Biol.* **201**, 2745–2751 (1998).
- Rall, J. A. *Exercise Sport Sci. Rev.* **13**, 33–74 (1985).
- Gatesy, S. M. *J. Morphol.* **240**, 115–125 (1999).
- Gatesy, S. M. & Biewener, A. A. *J. Zool.* **224**, 127–147 (1991).

Ecology

Mistletoe seed dispersal by a marsupial

The temperate forest that extends from 35° S to 55° S along the Pacific rim of southern South America is home to an endemic and threatened flora and fauna¹. Many species belong to lineages that can be traced back to ancient Gondwanaland^{2,3}, and there are some unusual interactions between plants and animals. Here we describe an exclusive association that involves the dispersal of the sticky seeds of a mistletoe by a marsupial, *Dromiciops australis*, endemic to this region — a task

previously thought to be carried out exclusively by birds.

Birds have been described as the animal dispersers of the shrubby stem-parasitic plants of the two most species-rich mistletoe families, Loranthaceae and Viscaceae^{4,5}. The mistletoe's aerial parasitic lifestyle imposes stringent requirements on reproduction by seed, so it is not surprising that bird–mistletoe interactions are highly specialized⁶. Efficient dispersal of mistletoes involves not only the ingestion and transport of the sticky seeds produced by these plants, but also their placement on the living branches of an appropriate host.

In the Lake District of southern Argentina, we found that *D. australis*—a nocturnal marsupial endemic to the northern portion of the temperate forests of southern South America⁷—is the exclusive disperser of the seeds of the loranthaceous mistletoe *Tristerix corymbosus*. Mature fruits of *T. corymbosus* are green (Fig. 1a), a colour often associated with mammalian dispersers⁸.

During 500 hours of observation, we saw no birds eat these fruits. Although we found seeds of different flesh-fruit species in the stomach contents of 61% of 296 mist-netted birds, these did not include any from *T. corymbosus*. We timed the removal of 92 fruits: 91 were removed at night, and only one during the day. Seeds were often deposited on vertical trunks of shrubs and small trees in patterns incompatible with typical bird behaviour (Fig. 1b).

Automatic cameras photographed two species of mammal, both nocturnal, in trees supporting mistletoe plants. Judging by these photographs, *D. australis* was more abundant ($n=101$ photographs) than the rodent *Irenomys tarsalis* ($n=23$). Of these two, apparently only *D. australis* eats and defecates intact seeds of *T. corymbosus* (Fig. 1c). In the field, 84% of 57 live-trapped marsupials defecated 1–31 *T. corymbosus* seeds each (mean, 6.3 seeds) while still in the traps. None of 13 live-trapped *I. tarsalis* defecated mistletoe seeds or consumed fruits while in captivity.

We found that *D. australis* is a highly efficient disperser of mistletoe seeds. Ten captive *D. australis* ate all ten *T. corymbosus* fruits offered to each of them within an hour, peeling off the exocarp with their forepaws and swallowing the rest whole, then defecating 98% of the ingested seeds ($n=653$) undamaged. In the field, we counted 192 seeds in or above seed traps and estimated that only about 10% of the seeds defecated by *D. australis* fall to the ground.

Passage of seeds through the marsupial's gut is critical for germination and development of a 'holdfast' (the disc-like swelling at the end of the radicle that effects its attachment to the host plant). Most seeds removed from the exocarp by hand failed to germinate, neither could they infect host plants.

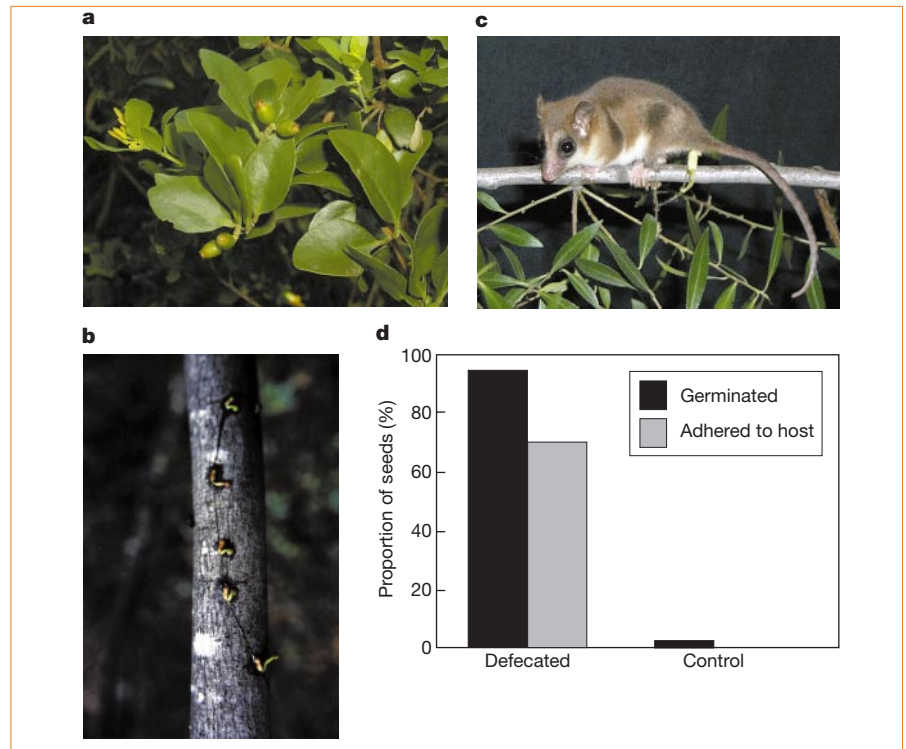


Figure 1 Seed dispersal of *Tristerix corymbosus*. **a**, Mature fruits, which measure about 1 × 0.6 cm, contain one seed measuring 0.7 × 0.4 cm. **b**, Germination of naturally dispersed seeds. Several seeds linked by a viscin thread are usually defecated in strings. These strings may stick to vertical trunks and branches, as shown, in spiral patterns around branches, or even to the underside of branches. Unlike other mistletoes which can only establish on thin branchlets^{5,12}, *T. corymbosus* can establish on branches and trunks up to 8 cm wide. **c**, A male *Dromiciops australis* (also known as the monito del monte), about 20 cm long from nose to tail tip, defecates a mistletoe seed. **d**, Percentage of seeds defecated by *D. australis* ($n=200$) and of seeds with the exocarp removed by hand ($n=200$; controls) that germinated and developed a holdfast that adhered to the host. We conducted the study in the Llaolao Reserve, Argentina (41° 8' S, 71° 19' W), during the 1998–99 and 1999–2000 fruiting seasons (December–March). The site supports an old-growth forest of *Nothofagus dombeyi*. The shrubs *Aristotelia chilensis* and *Maytenus boaria* are the main hosts of *T. corymbosus* in the study area. On 15 sampling dates, we tagged fruits for 24 h and checked them at dawn and at dusk. We mist-netted birds for 1,579 net-hours, and used water to flush the stomachs of all passerines. We live-trapped small mammals using single-door cage traps for 360 trap-nights. We monitored arboreal wildlife using two cameras for 90 d. During 1999–2000, we used six seed traps (2 × 2 m plastic sheet) to estimate the relative frequencies of naturally dispersed *T. corymbosus* seeds that stuck to plants or fell to the ground. At weekly intervals we counted new seeds falling on the sheets and those sticking to the branches overhead. Full details are available from the authors.

But over 90% of the seeds collected from marsupial faeces germinated. Most of these seeds also developed a holdfast that adhered to the host's bark (Fig. 1d).

Dromiciops australis is the only living representative of the family Microbiotheriidae, a marsupial lineage of presumed Gondwanan origin⁹. The Loranthaceae date back to the early to mid-Cretaceous⁵ and may likewise be of Gondwanan origin. In particular, *Tristerix* is considered to be one of the most primitive genera in this diverse family of nearly 1,000 extant species⁵, so the ancestors of *D. australis* could have been dispersing mistletoe seeds for more than 70 million years, before the breakup of western Gondwanaland. The bird lineages that disperse loranthaceous seeds originated no more than 20–25 Myr ago^{6,10}.

Our findings suggest that marsupial dispersal of mistletoe seeds might represent a very primitive mutualism in the Loranthaceae. Fossils of Palaeocene microbiotheriids found at different localities along the tropical Andes¹¹ may also indicate that the

marsupial–mistletoe mutualism described here was more widespread in the past.

Guillermo Amico, Marcelo A. Aizen

Laboratorio Ecotono, CRUB, Universidad Nacional del Comahue, Unidad Postal Universidad, 8400 San Carlos de Bariloche, Río Negro, Argentina
e-mail: marcito@crub.uncoma.edu.ar

- Armesto, J., Rozzi, R., Smith-Ramirez, C. & Arroyo, M. T. K. *Science* **282**, 1271–1272 (1998).
- Arroyo, M. T. K., Riveros, M., Peñaloza, A., Cavieres, L. & Faggi, A. M. in *High Latitude Rainforests and Associated Ecosystems of the West Coast of the Americas* (eds Lawford, R. G., Alaback, P. B. & Fuentes, E.) 134–172 (Springer, New York, 1996).
- Axelrod, D. I., Arroyo, M. T. K. & Raven, P. *Rev. Chil. Hist. Nat.* **64**, 413–446 (1991).
- Reid, N., Smith, M. S. & Yan, Z. in *Forest Canopies* (eds Lowman, M. D. & Nadkarni, N. M.) 285–310 (Academic, New York, 1995).
- Calder, M. & Bernhardt, P. (eds) *The Biology of Mistletoes* (Academic, New York, 1983).
- Reid, N. *Aust. J. Ecol.* **16**, 457–469 (1991).
- Marshall, L. G. *Mammal. Species* **99**, 1–5 (1978).
- van der Pijl, L. *Principles of Dispersal in Higher Plants* (Springer, Berlin, 1982).
- Springer, M. S. et al. *Proc. R. Soc. Lond. B* **265**, 2381–2386 (1998).
- Tambussi, C. & Noriega, J. *Münchener Geowiss. Abh.* **30**, 245–264 (1996).
- Goin, F. in *Vertebrate Paleontology in the Neotropics* (eds Kay, R. et al.) 185–204 (Smithsonian Institution, Washington DC, 1997).
- Sargent, S. *Funct. Ecol.* **9**, 197–204 (1995).