of injury during attitude control on water surfaces is minimal compared with that during gliding or crude flapping (the traditional model of insect flight evolution)[8]. Hind-leg skimming thus demonstrates how 'flight-ready' wing-beat kinematics and the ability to produce lift, thrust and the rudiments of attitude control might have evolved in a relatively safe setting before aerial flight in insects.

*Leuctra* stoneflies using hind-leg skimming attain speeds about 1.4 times faster than a taxonomically diverse sample of stoneflies that maintain water contact continuously with all six legs (Fig. 1). Higher speeds for hind-leg skimmers cannot be attributed to differences in body size (mean body lengths of *L. hippopus* and *L. sibleyi* are 6.5 and 5.0 mm respectively; the range for the other species tested is 4.5–8.0 mm; ANCOVA using body length as a covariate yields means of 36 cm $s^{-1}$ for hind-leg versus 25 cm $s^{-1}$ for six-leg skimmers; $P < 0.0001$).

Stoneflies tested at an air temperature of 12 °C can occasionally rise just above the water surface and fly. Velocity measurements of eight such events show that breaking free of the water and flying results in another 1.5-fold increase in forward speed compared with hind-leg skimming (using body length as a covariate for ANCOVA yields means of 56 versus 36 cm $s^{-1}$; $P < 0.0001$). Insects on water surfaces are exposed to predators, are displaced downstream by flowing water, and must often make headway against the wind, therefore faster skimming should generally enhance survival. Hind-leg skimming may be a favourable evolutionary transition from conventional skimming, with flight more favourable still. The various forms of surface locomotion used by modern stoneflies thus provide a detailed model for incremental improvements in aerodynamic locomotion that may have occurred during the evolution of flying insects from their aquatic ancestors.

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# Nitrification in Antarctic soils

Marshall[1] found pollen from trees (*Nothofagus* spp. and *Podocarpus* spp.) and the spores of several fungi not normally native to Antarctica in air samples collected at Signy Island in the maritime Antarctic. Their presence was associated with a specific weather pattern, occurring with an estimated mean annual frequency of 1.5, that allowed wind-borne transfer of exotic biological particles to Antarctica from South America. As Marshall pointed out, such events provide potential mechanisms for organisms to extend their ranges into Antarctica. These observations apparently indicate that Antarctica is not a continent in biological isolation. We suggest here that bacteria may have been dispersed throughout Antarctica in a similar way.

We have estimated the numbers of nitrifying (chemoautotrophic, $NH_4^+$-oxidizing) bacteria, and determined the short-term potential rates of nitrification (using the rate of $NO_2^-$ accumulation[2]) at 12 °C (typical summer surface soil temperature), in seven different soils collected from continental and maritime Antarctica during the 1994–95 Antarctic summer (Table 1).

Nitrifying bacteria were detected in all except two soils (4 and 5). In soils 1, 2, 6 and 7 the most probable numbers of nitrifiers[3] were low compared with temperate soils[2]. The most probable numbers of nitrifiers and the potential rate of nitrification in soil 3 were high and similar to those in temperate soils with high nitrification rates[2]. The potential nitrification rate in the other soils was either very low or not significant.

Soil 3 contained guano from an ancient penguin colony, as shown by our observation of remnants of Adélie penguin (*Pygoscelis adelie*) feathers and the fact that it contained substantially more nitrogen than five of the other six soils. The fact that there were inactive nitrifiers in four soils indicates their widespread distribution but that soil and/or other environmental conditions restricted activity and, therefore, proliferation.

Nitrifier activity in soil 3 was apparently related to the source of nitrifiable nitrogen. The temperature optimum for potential nitrification in this soil was between 22 °C and 25 °C, with the rate at 7 °C being less than 15% of the maximum, whereas that at 35 °C was 40% of the maximum. The relatively high temperature optimum for nitrification in soil 3 indicates that the nitrifiers were probably not of polar origin.

In the light of Marshall's demonstration[1] of wind-borne dispersal of pollen and spores to Antarctica, it seems highly likely that there might be simultaneous dispersal of bacteria. If such dispersal of bacteria occurs, nitrifiers could be deposited on soils both with and without nitrifiable nitrogen. Our observations indicate that environmental conditions in terrestrial Antarctica, rather than its geographical isolation, may determine the activity of particular groups of bacteria.

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Table 1 **Number of nitrifiers, potential nitrification rates and nitrogen content of Antarctic soils.**

| Soil | $Log_{10}$ MPN nitrifiers (per g soil) | Potential nitrification (nmol $g^{-1}$ $h^{-1}$) | Total soil nitrogen (μg $g^{-1}$) |
|---|---|---|---|
| 1 | 2.38 (2.08, 2.67) | 7.1 (0.58) | 90 (4.2) |
| 2 | 3.15 (2.86, 3.44) | 2.5 (0.75) | 250 (28) |
| 3 | 4.54 (4.25, 4.83) | 15.6 (4.92) | 310 (50) |
| 4 | ND | 2.7 (2.67) | 7 (0.7) |
| 5 | ND | 1.6 (4.02) | 38 (9.2) |
| 6 | 2.38 (2.08, 2.67) | 1.3 (0.71) | 37 (2.1) |
| 7 | −0.70 (−1.00, −0.40) | 1.5 (1.04) | 74 (5.9) |

Soil 1 was from Jane Coll, Signy Island in the South Orkney Islands (62° S, 45.5° W); soils 2–7 were all from sites on Alexander Island in continental Antarctica; soils 2 and 3 were from Rothera (67.5° S, 68° W); soil 4 was from Ablation Valley (71° S, 68° W); soils 5 and 6 were from Fossil Bluff (71.3° S, 68° W); soil 7 was from Ares Oasis (72° S, 68° W). The most probable numbers (MPN) of ammonium-oxidizers were determined with five replicates at each 10-fold dilution. Values in parentheses are 95% confidence limits[3]. ND, none detected. The potential nitrification rate is the rate of $NO_2^-$ accumulation in the presence of 0.5 mM $NH_4^+$ and $ClO_3^-$ (which inhibits $NO_3^-$ oxidation[2]) at 12 °C, per g soil per hour. The values for nitrification and total nitrogen are the means of three and two replicates, respectively, and the standard deviations are shown in parentheses.