Have mites (Acarina: Arachnida) colonised Antarctica and the islands of the Southern Ocean via air currents?

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ABSTRACT. Mites (Acarina: Arachnida) have not colonised Antarctica and the sub-Antarctic islands by ballooning on air currents. All acarine records from Pacific and Southern Ocean aerial plankton represent dead coastal (hemi)-edaphic species or phoretics dislodged from their flying insect hosts. The few sub-Antarctic records of mites capable of 'ballooning' on air currents are all verified as being attributed to anthropogenic introductions.

Contents

Introduction: colonisation of Southern Oceanic terrain

Pleistocene (1.8 million to 20,000 years before present) and earlier global cooling events have left a legacy of extremely impoverished polar and sub-polar non-marine faunas. The *c*. 35,000 North American Arctic/sub-Arctic invertebrate species include both pre-glacial relicts and post-glacial immigrants that 'diffused' into the region from the temperate Nearctic and Palearctic following the retreating northern ice sheets (Danks 1981, 1990). The equivalent Antarctic/sub-Antarctic faunas comprise a mere *c*. 1000, mostly mite (Acarina) and insect species (Pugh 1993; Chown and others 1998). Three factors have impoverished the Antarctic/Southern Ocean non-marine invertebrate faunas relative to their Arctic counterparts (Gressitt 1965; Chown and others 1998; Pugh, in press): the severe Antarctic climate, the 400–2000 km-wide barrier for potential colonists posed by the Southern Ocean, and the paucity of habitable ice-free terrain. The faunas are consequently largely pre-Pleistocene and endemic (Marshall and Pugh 1996; Pugh 1997, in press; Pugh and Convey 2000; Pugh and Scott 2002). So what evidence is there to support natural post-glacial colonisation?

The author has previously shown that humans are effective at transporting a range of mites to Antarctica and the islands of the Southern Ocean (Pugh 1994), yet birds and flying insects have not carried parasitic (dispersive and exsanguinating), phoretic (dispersive but non-feeding), or nidicolous (nest-dwelling) mites (Acarina: Arachnida) into the region (Pugh 1997). This paper considers the role of air currents as dispersal vehicles of these flightless arachnids.

Aerial plankton

The atmosphere of temperate regions contains a variable density (0.1–110 × 10^6 per km^2 to 4300 m) of flying and drifting airborne arthropods that constitute the 'aerial plankton' (White 1974; Bowden and Johnson 1976). Plankton density decreases geometrically from the coast to the open ocean as a result of both distance from source and behavioural mechanisms that prevent flying insects from being blown out to sea (Russell and Wilson 2001). Arthropods 'blown out to sea' are potential aerial colonists, although the distance they can travel is dependent upon flight capability.

Flying insects

Strong-flying Lepidoptera (moths) propelled by low-altitude (<600 m) trade winds, fronts, depressions, and hurricanes can complete very long-range ocean transits (Gressitt 1961; Gressitt and Yoshimoto 1963; Holzapfel 1978; Danks 1981). *Phytometra biloba* (Steph.) (Plusiidae) and *Vanessa cardui* (L.) (Nymphalidae) have crossed the *c*. 3600 km wide North Atlantic (Bowden and Johnson 1976), while both *V. cardui* and *Plutella xylostella* L. (Plutellidae) have been observed flying at <3000 km from land (Holzapfel and Harrell 1968; Holzapfel and others 1970). Wind-borne Lepidoptera have colonised isolated oceanic islands, including sub-Arctic Surtsey (*Agrotis ipsilon* (Hufnagel) — Noctuidae), sub-Antarctic South Georgia (*A. ipsilon*), Marion (*P. xylostella* and *V. cardui*), and Crozet (*V. cardui*) (Lindroth and others 1966; Voisin 1975; Bonner and Honey 1987; Chown and Language 1994). Four Australian Macrolepidoptera were blown 1500 km from Tasmania to Macquarie Island by 100+ km h^{-1} cold fronts in 15 hours, or as little as 10 hours if (as is likely) the insects were able to fly in the nocturnal temperature inversion that would have kept air temperature at 10+°C, within the functional range of flight muscle (Greenslade and others 1999).

The postulated maximal insect transit range of 3000–4000 km (Bowden and Johnson 1976) is broadly corroborated by tracking insects in storms (Hirst and Hurst 1967) and field estimates of flight speed (<20 km h^{-1}) (Greenslade and others 1999), although laboratory estimates of flight endurance — 20+ hours (Murata and Tojo 2002) — are limited to species that do not complete ocean transits. Flying at higher altitude (4000+ m) in high-speed (80 km h^{-1}) winds (Close and others 1978) is not possible because extreme low temperatures of −30 to −10°C at such altitude would impair the function of insect flight muscle (Holzapfel and Harrell 1968).

Strong-flying Lepidoptera are only a minor component of aerial plankton compared with small and weak-flying Diptera, Heteroptera, and Homoptera (Yoshimoto and others 1962; Harrell and Yoshimoto 1964; Bowden and Johnson 1976; Greenslade 1994). These light insects, and other small flightless arthropods, can be propelled short distances by gentle (5 km h^{-1}) sea-level breezes, or much longer distances (200–800 km) at higher altitude (4000 m), where they do not (indeed, cannot) fly but 'drift' passively for prolonged periods (Bowden and Johnson 1976).

Flightless insects and spiders

Collembola and homopteran nymphs together with spiders and lepidopteran larvae 'ballooning' on silk threads have been found <1000 km from landfall over the South Pacific (Close and others 1978). Similarly, most Southern Ocean flightless insects are small (<2 mm), with a low specific gravity, and so are amenable to wind transport (Gressitt 1964, 1965; Pryor 1964). Weather systems dictate both the flight path and ultimate destination of all airborne arthropods (Bowman and others 2002), so which weather systems provide the most effective dispersal agents of flightless species?

Small non-flying aphids (Homoptera: Hexapoda) and ballooning spiders (Araneae) require updrafts of 1.0+ ms^{-1} to become and remain airborne (Holzapfel 1978; Henschel and others 1995), although few weather systems can maintain such updraughts for long periods *and* transit oceans. Thermals will provide sufficient lift but contain powerful downdraughts and are confined over warm (day-time) terrain (Gilsen 1948; Holzapfel and Harrell 1968). Cold fronts and westerlies may last several days and travel thousands of kilometres across oceans, but generate little (<0.05 ms^{-1}) uplift, while trade winds are confined between latitudes 30°N and 30°S. Powerful (200–450 km h^{-1}) jet streams occur at the right latitude but at such high altitudes (7–12 km) that they cannot affect terrestrial uplift. Furthermore, only the most resistant plant spores and invertebrate 'resting stages' could survive the low air pressures (200–400 mbar) and freezing temperatures (−65 to −35°C) associated with such altitudes (Barry and Chorley 1998), even if uplifted by other weather systems.

Cyclones and similar powerful 'organised storms' are the only effective long-range vehicles suitable for small flightless arthropods (Close and others 1978; Barry and Chorley 1998). These may last several days, travel against prevailing winds, have continual strong (<35 ms^{-1}) internal turbulent updrafts from sea level to 10+ km and transit the Southern Ocean, albeit less frequently (*c*. 1.5 versus *c*. 40 per annum) than tropical seas (Marshall 1996). So whereas powerful flying insects need only fly to maintain buoyancy and can be propelled <3000 km by low-altitude fronts and depressions, small, weak-flying and flightless insects can travel <2000 km in powerful 'organised storms' that provide both a transit vehicle and buoyancy.

Atmospheric fall-out of all airborne arthropods is initiated by exhaustion and termination of flight behaviour (insects only), cooling, downdraughts, precipitation, storm-scrubbing, and storm extinction (Hurst 1969; Russell 1999). Few of the insects that transit the Southern Ocean actually survive, as most fall at sites lacking prerequisite resources or succumb to the extreme Antarctic climate (Gressitt and others 1961). But the aforementioned examples confirm that some insects have made successful transits to become established on Southern Ocean islands.

Small araneomorph spiders may balloon on extruded silk threads long enough to gain lift from thermals and updraughts (Greenstone 1990; Weyman 1993). Minute (<1 mg) 'spiderlings' dominate the non-insect aerial plankton (Dean and Sterling 1985), but, being juveniles, they have a low colonisation success. Thus most long-range aerial colonists are minute adult Araneidae, Lycosidae, Theridiidae, and especially Linyphiidae (Gressitt 1964; Forster 1971; Greenstone and others 1985), representing 81% of verified specimens collected over the Southern Ocean (see Table 1 references) and 46% of Southern Ocean species (Pugh, in press). The Southern Ocean spider fauna is primarily vicariant, yet some Linyphiidae on South Georgia and the genus *Myro* (Desidae) on the South Indian Ocean Prince Edward, Crozet, Kerguelen, and Heard archipelagoes can be justifiably attributed to ballooning (Pugh, in press). Aerial transport is, however, hazardous and no records of Southern Ocean aerial spiders can be verified as alive at capture (Gressitt and others 1961; Holzapfel and others 1970), while all Antarctic records refer to dead shipborne contaminants (Yoshimoto and others 1962; Forster 1964, 1970, 1971).

As a few spiders ballooning on silk threads have made successful transits of the Southern Ocean, could Acari do likewise if carried on frontal systems and storms? Previous investigations into the efficacy of aerial transport have focused on the composition of 'aerial plankton' and/or the winds most likely to explain species distributions (Gilsen 1948; Bernini 1990). This approach is inappropriate for the scant and poorly identified Southern Ocean data, so the author has adopted a different approach, based on identifying taxa common to two independent databases. First, the Bishop Museum (Honolulu) records of airborne arthropods collected over the Pacific and Southern Oceans

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Table 1. Acarina from oceanic 'aerial plankton.' Figures show numbers of individuals of each taxon compared with totals reported for each reference source. As: Ascidae; Pa: Parasitidae; Ur: Uropodidae (Gamasida); Ve: Veigaiidae; Bd: Bdellidae (Actinedida); Eu: Eupodidae; Ac: Acaridae; Ty: Tyroglyphidae (Acaridida); Or: (Oribatida); ?: unknown/not specified. Totals = numbers reported pre-1968; Sum totals uses the Holzapfel and Harrell (1968) review as a baseline. Totals do not add up to numbers quoted in Holzapfel and Harrell (1968), suggesting the inclusion of other, non-published data.

As	Pa	Ur	Ve	Bd	Eu	Ac	Ty	Or	?	Totals	Sum totals	Ocean	Landfall (km)	Reference
–	–	–	–	–	–	–	–	–	4	972		West Pacific	200	Gressitt (1961)
–	–	–	–	–	–	–	–	–	4	1054		Pacific	review	Gressitt and Yoshimoto (1963)
–	–	–	–	–	–	–	–	4	–	1275		South Pacific	100	Yoshimoto and Gressitt (1963)
–	–	–	–	–	–	–	–	–	4	169		South Pacific	review	Gressitt (1964)
1	–	–	–	–	–	–	–	–	–	3686		West Pacific	110	Harrell and Yoshimoto (1964)
–	–	1	–	1	1	1	–	–	–	315		Pacific	50–600	Harrell and Holzapfel (1966)
1	1	1	–	1	1	1	1	4	7		13,000	1957–68	review	Holzapfel and Harrell (1968)
1	–	–	–	–	–	–	–	–	–		695	Pacific	3	Holzapfel and Perkins (1969)
–	–	–	–	–	–	–	–	1	–		1934	Atlantic	–	Holzapfel and others (1970)
3	–	–	1	–	–	–	–	4	–		–‖–	South Atlantic	–	Holzapfel and others (1970)
–	–	–	–	–	–	–	–	–	1		–‖–	S. Pacific/Southern	640	Holzapfel and others (1970)
200	–	1	–	–	–	–	–	3	60		2781	Pacific	46–1093	Holzapfel and others (1978)
205	1	2	1	1	1	1	1	12	68		c.19,000	Acarina ≈ c.300/c.18,000 = 1.6% of aerial plankton		

from 1957 to 1978 (Table 1), and second, the catalogue to Antarctic/Southern Ocean Acari (Pugh 1993 and unpublished updates).

Airborne Acari

The suggestion that juvenile deuteronymphs of some *Glycyphagus* and *Lepidoglyphus* spp. (Glycyphagidae: Acaridida = Astigmata) use fan- or leaf-shaped setae as sails in strong air currents is doubtful (Evans 1992). Indeed only a few Phytoseiidae (Gamasida = Mesostigmata), Eriophyidae, and Tetranychidae (Actinedida = Prostigmata) can disperse by aeronauting (Glick 1939; Fleschner and others 1956; Mumcuoglu and Stix 1974; Washburn and Washburn 1984; Kennedy and Smitley 1985; Zhao and Amrine 1997). None of these families has been reported either from the Antarctic (Pugh 1993) or from oceanic aerial plankton (Table 1). Furthermore, all seven Southern Ocean records of *Sejulus plumosus* Oudemans 1905 (Phytoseidae) on Îles Crozet; *Bryobia praetiosa* (C.L. Koch 1836) (Tetranychidae) on South Georgia, Îles Kerguelen, and St Paul Island; *Bryobia* sp. (Tetranychidae) on Îles Crozet; *Tetranychus* sp. (Tetranychidae), on South Georgia; and an unknown Eriophyidae on Marion Island, refer to anthropogenic introductions (Pugh 1994; D. Marshall, personal communication).

None of the Table 1 records can be attributed to aeronauting. The Ascidae, Parasitidae, Uropodidae, and Veigaiidae (Gamasida), are probable phoretics (*sensu* Binns 1982), dislodged when their flying insect hosts were collected by sample nets or traps. Phoretic arachnids impose significant burdens upon their hosts, which are unable to transport them transoceanic distances (Pugh 1997), so these records must be of 'local' origin and not the products of long-range dispersal. Similarly all Bdellidae, Eupodidae (Actinedida), Acaridae, Tyroglyphidae (Acaridida = Astigmata), and Oribatida (= Cryptostigmata) relate to local coastal edaphic/hemiedaphic mites that were locally uplifted by storms and/or imported as shipborne (anthropogenic) contaminants.

Conclusion

Mites have been collected over the Pacific and Southern oceans, yet four lines of evidence refute acarine aerial colonisation of Antarctica and the sub-Antarctic islands. First, mites lack a life-history stage that could survive a long-range, high-altitude, airborne transit (Wallwork 1965; Marshall and Pugh 1996). Second, it is unlikely that the few Acari collected close to the Antarctic coast were alive at capture; indeed co-sampled arthropods were dead or even fragmented (Holzapfel and others 1970). Third, these, and all other mites trapped over the Pacific and Southern oceans, were either phoretics dislodged from locally dispersed flying insects and/or were locally uplifted by storms. And fourth, the principal aeronauting families of Phytoseidae, Eriophyidae, and Tetranychidae have not been recorded over the Pacific or Southern oceans, and all seven sub-Antarctic island records for these families refer to introduced aliens. Such evidence would appear to confirm Dalenius and Wilson (1958), in that anemohoria is 'a very perilous way of transport (which usually) ends with disaster.'

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