

Further support for thermal ecosystem engineering by wandering albatross

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Abstract: On sub-Antarctic Marion Island, wandering albatross (*Diomedea exulans*) nests support high abundances of tineid moth, *Pringleophaga marioni*, caterpillars. Previous work proposed that the birds serve as thermal ecosystem engineers by elevating nest temperatures relative to ambient, thereby promoting growth and survival of the caterpillars. However, only 17 days of temperature data were presented previously, despite year-long nest occupation by birds. Previous sampling was also restricted to old and recently failed nests, though nests from which chicks have recently fledged are key to understanding how the engineering effect is realized. Here we build on previous work by providing nest temperature data for a full year and by sampling all three nest types. For the full duration of nest occupancy, temperatures within occupied nests are significantly higher, consistently by *c.* 7°C, than those in surrounding soils and abandoned nests, declining noticeably when chicks fledge. Caterpillar abundance is significantly higher in new nests compared to nests from which chicks have fledged, which in turn have higher caterpillar abundances than old nests. Combined with recent information on the life history of *P. marioni*, our data suggest that caterpillars are incidentally added to the nests during nest construction, and subsequently benefit from an engineering effect.

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Introduction

Ecosystem boundaries are seldom impermeable. For example, extensive transfer of nutrients and energy takes place from terrestrial systems to the ocean, driving high primary and secondary marine productivity (Cloern *et al.* 2014). Similarly, terrestrial ecosystems receive marine-derived nutrients from aerosols, shore drift of algae and carrion, marine mammals, and seabirds (Polis *et al.* 2004). Seabirds, in particular, are important mediators of these interactions. They transfer energy and nutrients from the marine system when they come ashore to breed, moult or rest (Polis *et al.* 1997, Sánchez-Piñero & Polis 2000), and in doing so substantially influence ecosystem structure and function (Sánchez-Piñero & Polis 2000).

Seabirds also influence terrestrial systems in other ways, particularly as ecosystem engineers – organisms that modify resources available to other species by either their presence or actions, and thereby create, modify or maintain habitats (Wright & Jones 2006). Seabirds make their ecosystem engineering contribution largely through

the excavation of burrows and the construction of other forms of nests. These may result in the displacement of tons of material, creating new habitats for a range of other organisms (Bancroft *et al.* 2005).

On sub-Antarctic islands, seabirds are important in transferring nutrients from the sea to terrestrial systems (Smith 1978, Joly *et al.* 1987, Erskine *et al.* 1998). From burrowing petrels to the larger penguins and albatrosses, all surface and sub-surface nesters make significant nutrient transfers (Smith 2008), with profound influences on ecosystem structure and function (Crafford & Scholtz 1986, Joly *et al.* 1987, Gabriel *et al.* 2001, Vincke *et al.* 2007, Moravcová *et al.* 2010).

Sinclair & Chown (2006) proposed that the wandering albatross, *Diomedea exulans* L., serves as a thermal ecosystem engineer for caterpillars of the detritivorous, tineid moth, *Pringleophaga marioni* Viette. Caterpillar biomass is, on average, higher in recently abandoned albatross nests, and varies less among nests than it does in other habitats or older albatross nests occupied by the moth caterpillars. Because nutrient availability does not

differ appreciably between newer and older nests, it was suggested that the increased temperatures in occupied albatross nests favour caterpillar growth and survival. Sinclair & Chown (2006) indicated that incubating birds raise nest temperatures by *c.* 5°C compared with the surrounding soils. Limited recordings of nest temperatures suggest that they are close to the optimum temperature for caterpillar growth, and decrease the probability of repeated low temperature stresses which affect growth and survival (Sinclair & Chown 2005, 2006).

Despite the major empirical requirements of this thermal ecosystem engineering hypothesis being addressed in its initial formulation, two significant pieces of evidence were missing. First, the temperature record on which the assumption of elevated temperatures during incubation was based encompassed only 17 days in the autumn (April 2004). By contrast, wandering albatross nests are occupied for almost a full year (Ryan & Bester 2008). Therefore, the extent to which a beneficial temperature effect might be realized both across cooler and warmer periods of the year was not determined. Increased temperatures in cool periods could increase the advantage of the nest habitat, but *P. marioni* growth and survival decreases at and above 15°C, making extensive warming during the summer potentially problematic (Haupt *et al.* 2014a). If caterpillars are routinely exposed to temperatures which compromise their fitness, wandering albatross nests would clearly be more harmful than beneficial. Second, the original study compared caterpillar biomass in recently abandoned nests (as a

proxy for occupied nests which could not be sampled because doing so would disturb the birds) with old nests, making no distinction between nests from which chicks had fledged that season and older nests. This distinction is important because it can provide insight into the duration of the increased abundance of caterpillars in nests. For example, if caterpillar biomass or abundance is high in nests from which chicks have recently fledged (but low in older nests), it can be assumed that the ecosystem engineering effect lasts the entire year of incubation, given that the wandering albatross lays in mid-summer, with eggs hatching in March and birds fledging the next summer (December to February) (Ryan & Bester 2008). By contrast, if abundance or biomass is low in both the previous season's and older nests it suggests that the engineering effect is restricted to the period during which incubation is actually occurring, and declines shortly thereafter.

Here we address these gaps by providing temperatures from several nests across a full year of occupation and by comparing caterpillar abundances from old nests (chicks fledged or abandoned two or more seasons previously), those from which chicks have recently fledged (i.e. nests last warmed by birds *c.* 4 months previously; based on records from the long-term wandering albatross monitoring programme on the island, Ryan & Bester 2008), and those which have been recently abandoned due to egg loss or young chick mortality (i.e. nests warmed by birds *c.* 4–6 weeks prior to sampling). Our aim was to assess more comprehensively the extent to which the thermal ecosystem effect is being



Fig. 1. Wandering albatross (*Diomedea exulans*) nests on sub-Antarctic Marion Island illustrating the form and structure of the nests. Note in the occupied nests the presence of *Poa cookii*, and bryophytes incorporated into the nest shown in the top right image. The image on the bottom left is of a recently abandoned nest (note eggshell fragments in the bottom left corner of the image, and two clear mouse burrows), and the image on the bottom right is of a long-abandoned nest, now overgrown.

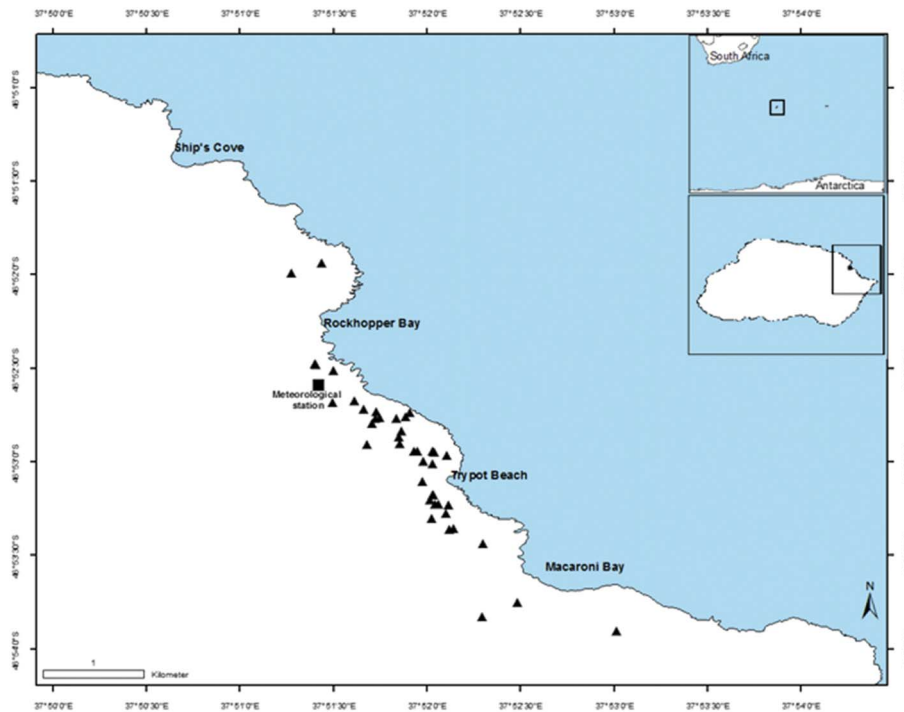


Fig. 2. Sampling locations of abandoned wandering albatross nests (triangles) along Marion Island's east coast between the meteorological station and Ship's Cove (to the north) and East Cape (to the south). The insets show the position of Marion Island in the Southern Ocean (top) and of the location of the study site on Marion Island (bottom).

realized and the duration of carry-over of the effect after chick fledging.

Materials and methods

Study site and species

Marion Island (46°54'S, 37°45'E) is part of the Prince Edward Island group. It is of volcanic origin, dominated by tundra and polar desert biomes, and has a mean annual temperature of *c.* 6.5°C, 1900 mm total annual precipitation, and a windy climate (Chown & Froneman 2008). The Prince Edward Islands support *c.* 7300 adult wandering albatrosses (*c.* 44% of the global population; Ryan & Bester 2008). Breeding pairs build nests comprising large mounds of vegetation and peat collected from the surrounding area (Fig. 1). A single egg is laid and incubated over the summer, hatches in March, is incubated until the brood-guard phase is over (*c.* 4–5 weeks later), and chicks fledge anytime between December and February (Ryan & Bester 2008). Therefore, nests are occupied for almost a full year. House mice have been introduced to Marion Island (Chown & Froneman 2008) and are associated with wandering albatross nests, affecting a small proportion of the chicks (Jones & Ryan 2010).

The flightless moth *Pringleophaga marioni* is endemic to the Prince Edward Islands, and, apart from their occurrence in wandering albatross nests, all life stages are found in a range of habitats from salt spray plant communities on the coast to microhabitats under stones,

and in mosses and cushion plants at elevations up to 800 m a.s.l. Larvae are most abundant in nutrient-enriched areas such as *Poa cookii* (Hook.f.) tussock grasslands and *Cotula plumosa* (Hook.f.) herbfield (Burger 1978, Crafford & Scholtz 1987). They have a mean critical thermal minimum (CT_{min}) of -0.6°C, freeze at -5.0°C, and show 100% survival of 12 h exposure to -6.0°C, but have 100% mortality after 18 h at -9.0°C (Klok & Chown 1997). Although they are moderately freeze-tolerant, repeated exposure to low temperatures reduces the growth rate of the caterpillars (Sinclair & Chown 2005). Recent evidence has also resolved the life-cycle duration of the species (Haupt *et al.* 2014a). At 10°C, egg duration is 4–7 weeks, larval duration *c.* 46 weeks and pupal duration *c.* 7 weeks, with a total life cycle of *c.* 1 year. Although larval duration is much reduced (to *c.* 17 weeks) at 15°C, survival is low.

Microclimate measurements

During the April–May relief voyage to Marion Island in 2011, ten occupied and ten abandoned wandering albatross nests were identified in the vicinity of the meteorological station and along the route to Macaroni Bay on the east coast (Fig. 2). Two calibrated iButton thermocron dataloggers (Model DS1922L, Maxim Integrated, Fairbridge, South Africa) were attached to plastic cable-ties (to make relocation possible) and were inserted mid-height into the side of each nest (*c.* 7–10 cm above the surrounding ground level). The loggers recorded temperature (0.5°C resolution) at hourly

intervals from May 2011 to March 2012. Care was taken not to damage the nest structure, and albatross researchers assisted with iButton deployment into occupied nests during their routine surveys. Soil temperature was recorded hourly at 2 cm depth by iButtons that were inserted in the side of plastic marker poles and placed into the soil 2 m away from each nest. For occupied nests, chick mortality or fledgling date was obtained from the albatross monitoring programme records (see Crawford & Cooper 2003 for programme description).

Sampling of nests and other habitats for caterpillars

During the April–May relief voyage in 2012, 43 abandoned wandering albatross nests were identified between the meteorological station on Marion Island's east coast to Ship's Cove in the north and East Cape to the south (Fig. 2), excluding the wandering albatross long-term study colony at Macaroni Bay to which general entry is not permitted. Nests were located mainly in dry or wet mire communities, or along *Blechnum penna-marina* slopes (Gremmen 1982). Following Sinclair & Chown (2006), only nests not currently occupied by birds were sampled. These were termed 'abandoned nests' and subsequently grouped into three types: i) old, nests that had not been occupied for most of 2011 or the previous seasons, ii) fledged, nests that had been occupied the previous season, i.e. built in November 2010 and from which chicks had fledged between December 2011 and January 2012, and iii) new, nests built for the current season, i.e. in November 2011, but had recently failed due to egg or young chick mortality. Researchers working over the 2011/2012 field season provided this information based on nest monitoring routinely conducted at the island. Fifteen new nests and fourteen of each of the fledged and old nests were selected as we came upon them and sampled across the area, within the constraints of the Prince Edward Islands Management Plan (Chown & Froneman 2008).

The height and the largest and smallest diameters of each nest were recorded, and the vegetation occurring on and surrounding the nest, the number of mouse burrows visible, and the distance from the coast were noted. The nest material was searched by hand for caterpillars by 2–4 samplers, who completely dismantled the nest and searched all of the material for caterpillars. No time limit was set on the search, which was typically completed in 1–2 hours, after which the material was replaced to form an *in situ* mound. Caterpillars were placed in groups of *c.* 20 in 350 ml plastic jars filled with nest material and returned to the laboratory within 6 hours of collection.

Caterpillars were then separated from the nest material, counted and weighed (0.1 mg resolution; Mettler AE163, Mettler-Toledo, Cape Town, South Africa), and returned within 24 h to the nests from which they were collected.

Individual caterpillar dry mass was estimated from a linear regression of dry on wet mass by using the mass of 138 individuals dried at 60°C (dry mass (g) = 0.113311 × wet mass (g); intercept = 0) provided by Sinclair & Chown (2005). Because caterpillars are usually concentrated in the surface layers of the nest (T.M. Haupt, S.L. Chown, personal observations), caterpillar biomass and density in nests were expressed as mg m⁻² and numbers m⁻², respectively, with the surface area of each nest calculated as the area of an ellipse.

Similar to Sinclair and Chown (2006), estimates of caterpillar biomass and density in nests in April and May 2012 were compared to those obtained from invertebrate surveys in April and May 1997 (Hänel 1999). Although a 15 year time difference exists between the habitat and albatross nest sampling events, the recent general decline in invertebrate densities in most habitats on Marion Island, largely owing to predation by introduced mice (Chown *et al.* 2002, Chown & Froneman 2008, also G.T.W. McClelland, A.E. Burger, R.J. van Aarde & S.L. Chown, unpublished data) biases our analysis against finding higher densities of caterpillars in nests. Dry caterpillar biomasses and numbers in nests were compared to those obtained by Hänel (1999) from hand-sorted 7 cm diameter soil cores on a per-surface-area basis. These previous data were collected in an island-wide stratified approach, covering the mire communities dominated

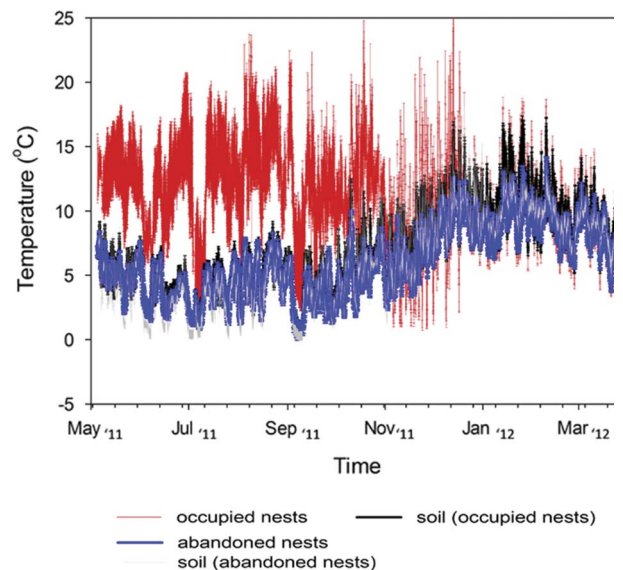


Fig. 3. Mean (\pm standard error) temperature recorded in occupied and abandoned wandering albatross nests and soil habitats adjacent to these nests from May 2011 to March 2012. Note that the period in December 2011 where temperatures begin to converge among nest types is coincident with the period when chicks begin venturing away from nests and fledge.

Table I. For each monthly temperature parameter, habitats which had significantly lower temperatures compared to occupied nests are shown. These are: soil adjacent to occupied nests (OS), abandoned nest (AN) and soil adjacent to abandoned nests (AS). Non-significant differences between occupied nests and other habitats are indicated by 'ns'. The single instance where temperatures were significantly lower in occupied nests compared to other habitats is indicated by * (for full statistical results see Supplemental Table S2 found at <http://dx.doi.org/10.1017/S0954102015000383>).

Month	Mean	Daily minimum	Daily maximum	Absolute minimum	Absolute maximum
May 2011	OS, AN, AS	OS, AN, AS	OS, AN, AS	OS, AN, AS	OS, AN, AS
Jun 2011	OS, AN, AS	OS, AN, AS	OS, AN, AS	OS, AN, AS	OS, AN, AS
Jul 2011	OS, AN, AS	OS, AN, AS	OS, AN, AS	OS, AN, AS	OS, AN, AS
Aug 2011	OS, AN, AS	OS, AN, AS	OS, AN, AS	OS, AN, AS	OS, AN, AS
Sept 2011	OS, AN, AS	OS, AN, AS	OS, AN, AS	ns	OS, AN, AS
Oct 2011	OS, AN, AS	OS, AN, AS	OS, AN, AS	OS, AN, AS	OS, AN, AS
Nov 2011	OS, AN, AS	ns	OS, AN, AS	ns	OS, AN
Dec 2011	OS, AN, AS	ns	OS, AN, AS	ns	OS, AN
Jan 2012	AN	ns	AN, AS	*	AN, AS
Feb 2012	ns	ns	AN, AS	ns	AN, AS
Mar 2012	AN	ns	AN, AS	ns	AS

by *Sanionia uncinatus* (Hedw.) or *Blepharidophyllum densifolium* (Hook.) Ångström ex C. Massal., and non-mires dominated by *P. cookii*, *C. plumosa* or *Crassula moschata* G.Forst.

Statistical analyses

Microclimate temperature data from occupied and abandoned nests, as well as adjacent soil habitats were divided into months, and for each month the mean, daily minimum and maximum, and absolute minimum and maximum temperatures were obtained. For each month, a generalized linear model (Gaussian distribution of errors, log link in the case of absolute minimum and maximum as data were skewed), implemented in R version 3.0.0 (R Development Core Team 2013), was used to compare temperature variables of occupied nests with those of abandoned nests and the adjacent soil habitats. For each nest and adjacent soil habitat, temperatures at which caterpillars are below their CT_{min} , i.e. $<0.2^{\circ}C$ (because of the CT_{min} range of $-1.6^{\circ}C$ to $0.1^{\circ}C$), supercooling point, i.e. $<-3.3^{\circ}C$ (because of the supercooling range of $-3.4^{\circ}C$ to $-7.1^{\circ}C$), and lower lethal temperature of $<-8.9^{\circ}C$ (based on 100% mortality at $-9^{\circ}C$; Klok & Chown 1997), were counted in Microsoft Excel (Microsoft, Seattle, WA, USA).

Caterpillar abundance (i.e. biomass and density) was compared among nest types (old, fledged and new) using a generalized linear model (assuming a quasi-Poisson distribution of errors following Crawley 2012) implemented in R version 3.0.0. Because of relatively high numbers of zero counts in the samples from non-nest vegetation types, caterpillar biomass and density were compared among new nests and the vegetation types using a hurdle model (with negative binomial distribution) (Zuur *et al.* 2009) implemented in R version 3.0.0 using the *pscl* library (Jackman 2014).

Results

Some iButtons failed to record or were irrecoverable, or the chick died soon after sampling of nest temperatures began (Fig. S1 found at <http://dx.doi.org/10.1017/S0954102015000383>), thus, temperature data were available for three occupied nests, eight soil habitats adjacent to occupied nests, five abandoned (fledged) nests and five soil habitats adjacent to abandoned nests. Temperatures in occupied nests were higher than in other habitats (Fig. 3) with a broad range of daily minimum and maximum temperatures (Table SI <http://dx.doi.org/10.1017/S0954102015000383>). Albatross research monitoring records indicate that the chicks began venturing away from the nests at the beginning of December and fledged at the end of the month. A decline in temperature of the now-vacant nests was noticeable at this point (Fig. 3). Whilst nests were occupied (May to December 2011) monthly temperature parameters (i.e. mean, daily minimum and maximum, and absolute minimum and maximum) were mostly significantly higher in occupied nests compared to adjacent soils, and compared to abandoned nests and adjacent soils (Table I).

Table II. Outcomes of the generalized linear models (negative binomial distribution of errors, log link function) comparing caterpillar biomass ($mg\ m^{-2}$) or density (numbers m^{-2}) in new, old and fledged nests.

	Estimate	Standard error	<i>z</i>	<i>P</i>
Biomass				
Intercept	7.042	0.194	36.238	<0.0001
Fledged	-2.350	0.281	-8.371	<0.0001
Old	-6.637	0.355	-18.713	<0.0001
Residual deviance: 48.068 on 40 degrees of freedom				
Density				
Intercept	4.653	0.167	27.812	<0.0001
Fledged	-2.236	0.252	-8.861	<0.0001
Old	-7.292	1.028	-7.092	<0.0001
Residual deviance: 35.606 on 40 degrees of freedom				

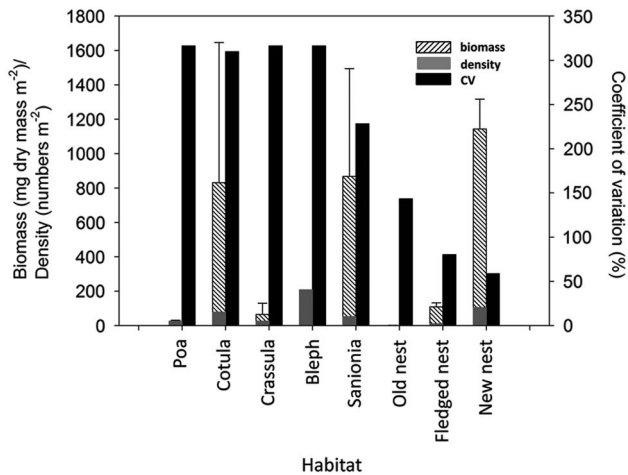


Fig. 4. Mean (\pm standard error) and coefficient of variation (CV) of biomass (mg m^{-2}) and density (numbers m^{-2}) of *Pringleophaga marioni* caterpillars in eight habitats on Marion Island. Five vegetation complexes sampled by Hänel (1999) in April or May 1997 (*Poa cookii*, *Cotula plumosa*, *Crassula moschata*, *Blepharidophyllum densifolium* and *Sanionia uncinatus*), and old, fledged and new nests sampled in this study.

After chicks had fledged (i.e. December 2011 and January 2012), there were mostly no significant differences in the monthly temperature parameters between these habitats (Table I), though where present these were between abandoned nests and soil sites, reflecting spatial variation in microclimate.

In occupied nests, CT_{\min} threshold events (temperatures $< 0.2^{\circ}\text{C}$) occurred on average 50 times over the course of the year compared to 420 in abandoned nests and 842 in

Table III. Outcome of the hurdle model comparing caterpillar biomass (mg m^{-2}) in new nests with that found in five vegetation complexes (*Blepharidophyllum densifolium*, *Cotula plumosa*, *Crassula moschata*, *Poa cookii* and *Sanionia uncinatus*) in April and May 1997 (Hänel 1999).

	Estimate	Standard error	z	P
Count model coefficients (truncated negative binomial with log link)				
Intercept	7.042	0.184	38.249	< 0.0001
<i>B. densifolium</i>	-1.485	0.739	-2.011	0.0443
<i>C. plumosa</i>	1.291	0.537	2.406	0.0161
<i>C. moschata</i>	-0.565	0.737	-0.767	0.4432
<i>P. cookii</i>	-1.992	0.740	-2.691	0.0071
<i>S. uncinatus</i>	1.333	0.537	2.485	0.0129
Log(theta)	0.678	0.281	2.416	0.016
Zero hurdle model coefficients (binomial with logit link)				
Intercept	19.570	4577.960	0.004	0.9970
<i>B. densifolium</i>	-21.760	4577.960	-0.005	0.9960
<i>C. plumosa</i>	-20.950	4577.960	-0.005	0.9960
<i>C. moschata</i>	-21.760	4577.960	-0.005	0.9960
<i>P. cookii</i>	-21.760	4577.960	-0.005	0.9960
<i>S. uncinatus</i>	-20.950	4577.960	-0.005	0.9960
Log-likelihood: -195.5 on 13 degrees of freedom				

Table IV. Outcome of the hurdle model comparing caterpillar density (numbers m^{-2}) in new nests with that found in five vegetation complexes (*Blepharidophyllum densifolium*, *Cotula plumosa*, *Crassula moschata*, *Poa cookii* and *Sanionia uncinatus*) in April and May 1997 (Hänel 1999).

	Estimate	Standard error	z	P
Count model coefficients (truncated negative binomial with log link)				
Intercept	4.653	0.142	32.848	< 0.0001
<i>B. densifolium</i>	2.986	0.559	5.346	< 0.0001
<i>C. plumosa</i>	1.313	0.409	3.212	0.0013
<i>C. moschata</i>	0.907	0.562	1.616	0.1062
<i>P. cookii</i>	0.907	0.562	1.616	0.1062
<i>S. uncinatus</i>	0.907	0.410	2.216	0.0267
Log(theta)	1.238	0.302	4.080	< 0.0001
Zero hurdle model coefficients (binomial with logit link)				
Intercept	19.570	4577.960	-0.004	0.9970
<i>B. densifolium</i>	-21.760	4577.960	-0.005	0.9960
<i>C. plumosa</i>	-20.950	4577.960	-0.005	0.9960
<i>C. moschata</i>	-21.760	4577.960	-0.005	0.9960
<i>P. cookii</i>	-21.760	4577.960	-0.005	0.9960
<i>S. uncinatus</i>	-20.950	4577.960	-0.005	0.9960
Log-likelihood: -147.1 on 13 degrees of freedom				

soil habitats. The large number of events in the soils and abandoned nests reflect the repeated passing of the threshold given average temperatures close to zero in the winter months and unpredictability of temperature change at the island (Chown & Froneman 2008). The temperatures in nests or soils never reached the thresholds at which freezing ($< -3.3^{\circ}\text{C}$) or death (lower lethal temperature $< -8.9^{\circ}\text{C}$) occur.

Caterpillar biomass and density in new nests was significantly higher than in old and fledged nests (Table II, Fig. 4). Moreover, the coefficient of variation of caterpillar biomass in new nests was lower than that found for fledged and old nests (Fig. 4). Compared to vegetation complexes sampled in April and May 1997, caterpillar biomass in new nests was significantly lower than in *S. uncinatus* and *C. plumosa*, no different than in *C. moschata*, and significantly higher than in *B. densifolium* and *P. cookii* (Table III). Caterpillar density in new nests was significantly lower compared to *S. uncinatus*, *C. plumosa* and *B. densifolium*, and no different to that found in *C. moschata* and *P. cookii* (Table IV). By contrast, the coefficient of variation in nests, and new nests in particular, was 5–6 fold lower, in the latter case significantly (Fligner-Killeen test: $X^2 = 102.5786$, $df = 16$, $P < 0.0001$), than in all other habitats (Fig. 4).

Discussion

Here we extend previous observations (Sinclair & Chown 2006) to show that wandering albatross nests are warmer than surrounding habitats for the duration of the albatross incubation period, and that this increased temperature substantially decreases the incidence of

events below the CT_{\min} of caterpillars. Like Sinclair & Chown (2006), we also find higher biomass and lower variance of caterpillars in new versus older nests. However, dividing the 'old' nests into those which fledged chicks and those which are more than one season old reveals that the decline in caterpillar abundance once the albatrosses leave is rapid (within several months), suggesting a relatively short cycle during which the nest harbours a high density of caterpillars. These observations are consistent with both the *c.* 1 year life cycle proposed by Haupt *et al.* (2014a), and the thermal ecosystem engineering hypothesis.

Unlike the previous investigation, which proposed the thermal ecosystem engineer hypothesis (Sinclair & Chown 2006), we found that caterpillar abundance or biomass is not always higher in newly abandoned nests than in other non-nest habitats. Why is this the case? First, the finding might be a consequence of the difference in sampling methods between those used for nests and those used in the habitat surveys undertaken previously (Hänel 1999). The former included a relatively large area (whole nests, on average 7010 cm²) whereas the latter include quite small areas (7 cm diameter cores, area of 38.5 cm²) which are then scaled up to provide caterpillar abundance per m². Indeed, larger census areas tend to bias density estimates downwards (Gaston *et al.* 1999), and this may have had an effect here, though the same effect should have been realized for the previous investigation. Second, it is clear that abundances are naturally dynamic and expected to vary from year to year, even though previous studies have suggested lower, short-term interannual abundance variation characterizes many arthropod species on Marion Island compared with those elsewhere (Crafford *et al.* 1986, Barendse & Chown 2001). Alternatively, declining abundances across the island associated with the impact of house mice and their use of different habitats (Chown *et al.* 2002, Smith *et al.* 2002) might also be causing variation in abundances among years. Nonetheless, the consistently low coefficient of variation in biomass/density among new nests, compared with other nest types and non-nest habitats, is in keeping with Sinclair & Chown (2006). It shows, together with relatively high abundances, that new nest habitats are consistently good habitats for caterpillars, and more so than might be expected for any other habitat type sampled on the island. In consequence, it appears that wandering albatrosses do serve as ecosystem engineers, although the magnitude of the effect is likely to vary among individual nests.

The thermal ecosystem engineering hypothesis relies on increased temperatures (closer to optima for caterpillar growth and survival) for the duration of incubation (Sinclair & Chown 2006). Our year-long temperature dataset confirms that this is the case for the entire period that nests are occupied. Whilst nests were fully occupied

(i.e. between May 2011 and November 2012), mean temperatures were anywhere between 8°C and 16°C. By contrast, mean temperatures in abandoned nests and surrounding soils were between 3°C and 10°C during the monitoring period, and when nests were abandoned, or once chicks left the nest, temperatures rapidly converged with those of the surrounding environment. Thus, caterpillars in occupied nests are less likely to encounter critical temperatures that limit activity and are likely to be consistently closer to optima for growth, than caterpillars in other environments. Although temperatures in nests occasionally reach values that are inimical to growth (i.e. $\geq 15^\circ\text{C}$), fluctuating temperatures that include these higher values have less impact than constant exposure to these temperatures and seem to result in growth that is close to the optimum rate, with minimal impact on survival (at a fluctuating temperature of 5–15°C the larval stage is 37 weeks) (Haupt *et al.* 2014a; see also Colinet *et al.* 2015 for general discussion of fluctuating temperatures).

We expect that these increased nest temperatures will lead to faster development of caterpillars. Based on a sum of effective temperatures of 227 degree days for completion of the larval stage, with a lower development threshold of 0.8°C (Haupt *et al.* 2014a), the temperature data suggest that caterpillars are likely to complete their life cycle within 30 weeks in occupied nests, but in about a year in unoccupied nest (or non-nest) habitats. This increase in development time is consistent with the thermal ecosystem engineering hypothesis, and also with the relatively low caterpillar abundance in nests from which chicks have fledged. We expect that the majority of caterpillars from those nests have already completed development and left the nest at the time of sampling.

An alternative explanation for the rapid decrease in caterpillar abundance is that albatross adults and later on chicks themselves discourage introduced house mice, which are major predators of *P. marioni* caterpillars (Smith *et al.* 2002), from occupied nests, reducing caterpillar predation pressure. However, numbers of mouse burrows do not differ among nest categories (mean \pm standard deviation (*n*), old: 1.6 \pm 1.8 (14); fledged: 2.3 \pm 2.7 (14); new: 3.1 \pm 3.0 (15); generalized linear model, quasi-poisson distribution, $P > 0.44$), and the impact of mice on albatross chicks (Jones & Ryan 2010) suggests that albatross presence does not particularly deter the activities of mice at the nest.

The low abundance of caterpillars in nests that have not been recently occupied suggests that there is differential colonization of newly-built albatross nests. Information on caterpillar chemosensory and thermal cue responses show that they are unlikely to seek out nests actively (Haupt *et al.* 2014b). It is not known whether adult moths seek out oviposition sites, as is common in other

Lepidoptera, but given the short lifespan and low vagility of the adult female moths (Crafford *et al.* 1986), coupled with the presence of *P. marioni* larvae across a range of habitats far from albatross nests (Burger 1978, Crafford *et al.* 1986), this seems unlikely (Haupt *et al.* 2014b). An alternative explanation is that caterpillars or eggs are serendipitously incorporated into the nests as adult albatrosses construct them from the surrounding vegetation (Warham 1990, Ryan & Bester 2008), which often includes *P. cookii* and bryophytes such as *B. densifolium* (observation of 60 nests indicated that *P. cookii* was used for construction of 49 of the nests and mosses in the same number, though not necessarily the same nests; data available on request) which have high densities or biomasses of caterpillars (Burger 1978, Crafford & Scholtz 1987, Chown *et al.* 2002).

Indeed, this can be estimated based on what is known of albatross nest size and caterpillar biomass per m². The mean volume of a new nest is 175 235 cm³ ($n = 15$). To construct such a nest, assume an albatross would need to collect 8.7 times the volume of a standardized area used for expressing caterpillar biomass (i.e. 1 m² × 2 cm, assuming caterpillars occupy only the top 2 cm of substrate, which = 20 000 cm³). Assume that, from Hänel's (1999) data, caterpillar density is on average 26 caterpillars per m³ in *P. cookii*-dominated or 52 caterpillars per m³ in *S. uncinata* bryophyte-dominated habitats. This suggests that albatrosses might incidentally collect somewhere between 230 and 450 caterpillars during their activity. Making the conservative assumption that somewhere between 10 and 50% of individuals actually end up being incorporated into nests, this suggests that nests should have somewhere between 23 and 200 caterpillars. Our counts from new nests vary between 33 and 148. The estimates are within the same order of magnitude, suggesting that the idea is plausible. Once caterpillars or eggs are added to the nests, favourable nest conditions improve caterpillar growth and survival. Thus, although it is clear that a thermal ecosystem engineering effect on caterpillar performance is realized, the high abundance in nests may be serendipitous.

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Author contribution

SLC & BJS designed the research. TMH, BJS, JDS & SLC undertook the research. TMH & SLC undertook the statistical analyses. All authors contributed to writing of the manuscript.

Supplemental material

A supplemental figure and two tables will be found at <http://dx.doi.org/10.1017/S0954102015000383>.

References

- BANCROFT, W.J., GARKAKLIS, M.J. & ROBERTS, J.D. 2005. Burrow building in seabird colonies: a soil-forming process in island ecosystems. *Pedobiologia*, **49**, 149–165.
- BARENDSE, J. & CHOWN, S.L. 2001. Abundance and seasonality of mid-altitude fellfield arthropods from Marion Island. *Polar Biology*, **24**, 73–82.
- BURGER, A.E. 1978. Terrestrial invertebrates: a food resource for birds at Marion Island. *South African Journal of Antarctic Research*, **8**, 87–99.
- CHOWN, S.L. & FRONEMAN, P.W. 2008. *The Prince Edward Islands. Land-sea interactions in a changing ecosystem*. Stellenbosch: Sun Press, 450 pp.
- CHOWN, S.L., MCGEOCH, M.A. & MARSHALL, D.J. 2002. Diversity and conservation of invertebrates on the sub-Antarctic Prince Edward Islands. *African Entomology*, **10**, 67–82.
- CLOERN, J.E., FOSTER, S.Q. & KLECKNER, A.E. 2014. Phytoplankton primary production in the world's estuarine-coastal ecosystems. *Biogeosciences*, **11**, 2477–2501.
- COLINET, H., SINCLAIR, B.J., VERNON, P. & RENAULT, D. 2015. Insects in fluctuating thermal environments. *Annual Review of Entomology*, **60**, 123–140.
- CRAFFORD, J.E. & SCHOLTZ, C.H. 1986. Impact of *Embryonopsis halticella* Eaton larvae (Lepidoptera: Yponomeutidae) feeding in Marion Island tussock grassland. *Polar Biology*, **6**, 191–196.
- CRAFFORD, J.E. & SCHOLTZ, C.H. 1987. Quantitative differences between the insect faunas of sub-Antarctic Marion and Prince Edward Islands: a result of human intervention? *Biological Conservation*, **40**, 255–262.
- CRAFFORD, J.E., SCHOLTZ, C.H. & CHOWN, S.L. 1986. The insects of sub-Antarctic Marion and Prince Edward Islands with a bibliography of entomology of the Kerguelen Biogeographical Province. *South African Journal of Antarctic Research*, **16**, 42–84.
- CRAWFORD, R.J.M. & COOPER, J. 2003. Conserving surface-nesting seabirds at the Prince Edward Islands: the roles of research, monitoring and legislation. *African Journal of Marine Science*, **25**, 415–426.
- CRAWLEY, M.J. 2012. *The R book*, 2nd ed. Chichester: John Wiley & Sons, 1076 pp.
- ERSKINE, P.D., BERGSTROM, D.M., SCHMIDT, S., STEWART, G.R., TWEEDIE, C.E. & SHAW, J.D. 1998. Subantarctic Macquarie Island: a model ecosystem for studying animal-derived nitrogen sources using ¹⁵N natural abundance. *Oecologia*, **117**, 187–193.
- GABRIEL, A.G.A., CHOWN, S.L., BARENDSE, J., MARSHALL, D.J., MERCER, R.D., PUGH, P.J.A. & SMITH, V.R. 2001. Biological invasions of Southern Ocean islands: the Collembola of Marion Island as a test of generalities. *Ecography*, **24**, 421–430.
- GASTON, K.J., BLACKBURN, T.M. & GREGORY, R.D. 1999. Does variation in census area confound density comparisons? *Journal of Applied Ecology*, **36**, 191–204.

- GREMMEN, N.J.M. 1982. *The vegetation of the subantarctic islands Marion and Prince Edward*. The Hague: W. Junk, 164 pp.
- HÄNEL, C. 1999. *The distribution and abundance of macro-invertebrates in the major vegetation communities of Marion Island and the impact of alien species*. MSc thesis, University of Pretoria, South Africa, 121 pp. [Unpublished].
- HAUPT, T.M., CRAFFORD, J.E. & CHOWN, S.L. 2014a. Solving the puzzle of *Pringleophaga* – threatened, keystone detritivores in the sub-Antarctic. *Insect Conservation and Diversity*, **7**, 308–313.
- HAUPT, T.M., SINCLAIR, B.J. & CHOWN, S.L. 2014b. Chemosensory and thermal cue responses in the sub-Antarctic moth *Pringleophaga marioni*: do caterpillars choose wandering albatross nest proxies? *Polar Biology*, **37**, 555–563.
- JACKMAN, S. 2014. *Package 'pscl'*. Available at: <https://cran.r-project.org/web/packages/pscl/pscl.pdf>.
- JONES, M.G.W. & RYAN, P.G. 2010. Evidence of mouse attacks on albatross chicks on sub-Antarctic Marion Island. *Antarctic Science*, **22**, 39–42.
- JOLY, Y., FRENOT, Y. & VERNON, P. 1987. Environmental modifications of a subantarctic peat-bog by the wandering albatross (*Diomedea exulans*): a preliminary study. *Polar Biology*, **8**, 61–72.
- KLOK, C.J. & CHOWN, S.L. 1997. Critical thermal limits, temperature tolerance and water balance of a sub-Antarctic caterpillar, *Pringleophaga marioni* (Lepidoptera: Tineidae). *Journal of Insect Physiology*, **43**, 685–694.
- MORAVCOVÁ, A., BEYENS, L. & VAN DE VIJVER, B. 2010. Diatom communities in soils influenced by the wandering albatross (*Diomedea exulans*). *Polar Biology*, **33**, 241–255.
- POLIS, G.A., ANDERSON, W.B. & HOLT, R.D. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics*, **28**, 289–316.
- POLIS, G.A., SÁNCHEZ-PINERO, F., STAPP, P.T., ANDERSON, W.B. & ROSE, M.D. 2004. Trophic flows from water to land: marine input affects food webs of islands and coastal ecosystems worldwide. In POLIS, G.A., POWER, M.E. & HUXE, G.R., eds. *Food webs at the landscape level*. Chicago: University of Chicago Press, 200–216.
- R DEVELOPMENT CORE TEAM. 2013. *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Available at: <http://www.R-project.org>, accessed 3 April 2013.
- RYAN, P.G. & BESTER, M.N. 2008. Pelagic predators. In CHOWN, S.L. & FRONEMAN, P.W., eds. *The Prince Edward Islands. Land-sea interactions in a changing ecosystem*. Stellenbosch: Sun Press, 121–164.
- SÁNCHEZ-PINERO, F. & POLIS, G.A. 2000. Bottom-up dynamics of allochthonous input: direct and indirect effects of seabirds on islands. *Ecology*, **81**, 3117–3132.
- SINCLAIR, B.J. & CHOWN, S.L. 2005. Deleterious effects of repeated cold exposure in a freeze-tolerant sub-Antarctic caterpillar. *Journal of Experimental Biology*, **208**, 869–879.
- SINCLAIR, B.J. & CHOWN, S.L. 2006. Caterpillars benefit from thermal ecosystem engineering by wandering albatrosses on sub-Antarctic Marion Island. *Biology Letters*, **2**, 51–54.
- SMITH, V.R. 1978. Animal-plant-soil nutrient relationships on Marion Island (sub-Antarctic). *Oecologica*, **32**, 239–253.
- SMITH, V.R. 2008. Terrestrial and freshwater primary production and nutrient cycling. In CHOWN, S.L. & FRONEMAN, P.W., eds. *The Prince Edward Islands. Land-sea interactions in a changing ecosystem*. Stellenbosch: Sun Press, 181–214.
- SMITH, V.R., AVENANT, N.L. & CHOWN, S.L. 2002. The diet and impact of house mice on a sub-Antarctic island. *Polar Biology*, **25**, 703–715.
- VINCKE, S., VAN DE VIJVER, B., LEDEGANCK, P., NIJS, I. & BEYENS, L. 2007. Testacean communities in perturbed soils: the influence of the wandering albatross. *Polar Biology*, **30**, 395–406.
- WARHAM, J. 1990. *The petrels, their ecology and breeding systems*. London: Academic Press, 452 pp.
- WRIGHT, J.P. & JONES, C.G. 2006. The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. *BioScience*, **56**, 203–209.
- ZUUR, A.F., IENO, E.N., WALKER, N., SAVELIEV, A.A. & SMITH, G.M. 2009. *Mixed effects models and extensions in Ecology with R*. New York, NY: Springer, 600 pp.