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From sea to land: assessment of the bio-transport of phosphorus by penguins in Antarctica*

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Abstract In Antarctica, the marine ecosystem is dynamically interrelated with the terrestrial ecosystem. An example of the link between these two ecosystems is the biogeochemical cycle of phosphorus. Bio-vectors, such as penguins, transport phosphorus from sea to land, play a key role in this cycle. In this paper, we selected three colonies of penguins, the most important seabirds in Antarctica, and computed the annual quantity of phosphorus transferred from sea to land by these birds. Our results show that adult penguins from colonies at Ardley Island, the Vestfold Hills, and Ross Island could transfer phosphorus in the form of guano at up to 12 349, 167 036, and 97 841 kg/a, respectively, over their breeding period. These quantities are equivalent to an annual input of 3.96×10^{9}–1.63×10^{10} kg of seawater to the land of Antarctica. Finally, we discuss the impact of phosphorus on the ice-free areas of the Antarctica.

Keyword: Southern Ocean; sea-land ecosystem; phosphorus cycle; penguin; guano

1 INTRODUCTION

Adjacent ecosystems interact with each other dynamically. For example, oceans and neighboring landmasses are linked by flows of materials, energy, and information. The flow of materials can be bi-directional. Nutrient-poor marine ecosystems may subsidize terrestrial ecosystems with certain nutrients. For example, seabirds from oligotrophic marine environments can increase nitrogen availability to primary producers and consumers on land, and significantly impact plant communities (Harrison, 2006). However, with few exceptions, the direction of material flow is from productive to unproductive ecosystems (Fariña et al., 2003).

Material transfer between ecosystems occurs via physical and biological vectors. The main physical vectors are water and wind, which transport material through advection or diffusion (Polis et al., 1997). Such allochthonous transport relies heavily on the permeability of ecosystem boundaries and characteristics including speed and volume of water and wind (Fariña et al., 2003). For example, wind speed is proportional to the amount of mineral salts transported by wind to the ice-free areas of Antarctica (Nędzarek and Rakusa-Suszczewski, 2007; Nędzarek, 2008). On the other hand, biological vectors are mobile consumers that feed in one habitat but excrete in another (Polis et al., 1997). Marine mammals and seabirds are vital for linking marine and terrestrial ecosystems (Sánchez-Piñero and Polis, 2000). They forage in marine habitats and breed on land, acting as

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important biological vectors carrying marine-derived nutrients or contaminants onto land (Sun and Xie, 2001; Blais et al., 2005; Keatley et al., 2007). The mobility, behavior, and physiology of these marine animals determine the efficiency of the delivery of nutrients; for example, biological mobility has direct impacts on the volume and spatial distribution of transported nutrients (Fariña et al., 2003).

Because of their ability to deliver nutrients from sea to land and to enhance the availability of local resources, seabirds have been the focus of many studies of nutrient transfer (Vidal et al., 2003). In cold and high latitude regions, the environment is relatively primitive and sensitive to the periodic migration of marine mammals and seabirds. In particular, many migratory animals in high latitude environments converge on biological oases such as ponds or polynyas; therefore, biological transport by marine mammals and seabirds is of particular significance in these regions (Blais et al., 2007).

The Southern Ocean is nutrient rich, and its surface water contains a high level of phosphate, except when phytoplankton blooms deplete phosphate at a local scale (Ducklow et al., 2007). Penguins, seals, and other animals forage in the Southern Ocean and breed on land. During the breeding season, they deposit a substantial amount of phosphorus into the terrestrial ecosystem in the form of guano, debris, eggshells, and feathers. This phosphorus enriches the low-productivity land of the Antarctic continent. The accumulation of a large amount of phosphorus-rich guano forms ornithogenic soil (Tatur and Myrcha, 1984). Carried by melting ice and snow or directly discharged (Hodson et al., 2010), ornithogenic soil and seabird guano can be deposited into lakes (Zhu et al., 2006a). Furthermore, wind can transfer marine macroalgae from waters of the inshore zone to the terrestrial environment. For example, in Admiralty Bay, macroalgae are the main source of phosphorus, nitrogen, and organic matter transported by physical vectors, and the total phosphorus released from macroalgae is 1.37–13.4 g/kg of dry mass (Nędzarek and Rakusa-Suszczewski, 2004).

The phosphorus derived from ornithogenic soils or guano is transported to the sea in streams or underground water. Wind and water also play an important role in transporting phosphorus from inland areas to the sea. Previous studies have shown that surface runoff containing guano and the decay of marine macroalgae are the main sources of phosphorus transfer to inshore ecosystems, thereby promoting the growth of phytoplankton (Rakusa-Suszczewski, 2003; Nędzarek and Rakusa-Suszczewski, 2004; Nędzarek, 2008).

The emission of phosphine formed in seabird rookeries to the atmosphere, and the deposition of phosphorus by atmospheric precipitation onto ice-free areas of Antarctica, are negligible (Zhu et al., 2006b; Nędzarek and Rakusa-Suszczewski, 2007). Therefore, the phosphorus biogeochemical cycle in Antarctica consists mainly of the movement of phosphorus among the sea, land, lakes, and streams. Seabird-derived phosphorus plays a dominant role in this cycle, and its quantification is critical for studying the ecosystems of Antarctica.

In this paper, we estimated the contribution of penguin guano to phosphorus transfer from the sea to ice-free areas, and discussed the major factors controlling phosphorus transfer. We then discussed the impact of phosphorus on the terrestrial and freshwater ecosystems of Antarctica.

2 MATERIAL AND METHOD

2.1 Study material and area

Penguins are the dominant seabird species in Antarctica. As seabirds, the ocean provides penguins with their only food source, and the birds spend more than half of their life at sea. Gentoo penguins (*Pygoscelis papua*), Adélie penguins (*Pygoscelis adeliae*), and Chinstrap penguins (*Pygoscelis antarctica*) breed on the Antarctic continent during the warm austral summer (from November to February). On the contrary, Emperor penguins (*Aptenodytes forsteri*) breed on the ice over winter (Korczak-Abshire, 2010), and do not transfer phosphorus from the ocean to land during their breeding period. Therefore, we did not include this species in our study.

We estimated the amount of phosphorus in penguin guano in three important penguin colonies, at Ardley Island in the South Shetland Islands and the Vestfold Hills and Ross Island in East Antarctica. The colonies in the Vestfold Hills and Ross Island are mainly populated by *P. adeliae*, and the Ardley Island colony by *P. papua*, *P. adeliae*, and *P. antarctica*. According to a survey in the summer of 2006/2007, as few as 10 pairs of adult *P. antarctica* were nesting at Ardley Island (Sun et al., 2010), so the phosphorus transported by this penguin species is likely to be negligible compared with other species and was not considered in further analysis.

2.2 Method

Currently, there are two main methods used for estimating the amount of nutrients transferred by birds. In the first method, described by Myrcha and Tatur (1991), several parameters were used to estimate the amount of phosphorus transported by Pygoscelid penguins from the sea to land during the nesting period in Antarctica. These parameters included food intake, chemical composition of excreta, duration of the reproductive period, and breeding success. This method assesses the total amount of phosphorus transferred by both adult and young penguins. However, during the breeding season, the efficiencies of food absorption differ for adults and chicks (Trivelpiece et al., 1987), so the phosphorus content and fecal production also differ. Furthermore, breeding productivity can be disturbed by human visitation (Lynch et al., 2010) and other factors, introducing substantial uncertainty in phosphorus content estimation. Therefore, in this study we ignored the phosphorus transferred by penguin chicks.

In the second method presented by Manny et al. (1994), the annual contribution of nutrients from waterfowl guano to lakes was estimated as the product of three factors: the amount of time spent on the lake for each species (use-days), defecation rates (the product of the mean number of droppings per day and mean weight per dropping), and the nutrient content of the guano. In that study, the product of the monthly average population of birds and the estimated days that each kind of waterfowl was present equaled their monthly effective use of the lake, and the sum of monthly effective use-days equaled the total annual effective use of the lake by each species of waterfowl (Manny et al., 1994). This method used four factors in calculating the annual amount of nutrient transferred to lakes by waterfowl, and we adopted this method for the current study.

For Adélie and Gentoo penguins, time spent each year on ice-free areas is relatively stable and guano excretion is a continuous process during the breeding period (Ainley, 2002). Consequently, we computed the amount of phosphorus (Q, kg/a) transferred from ocean to land in the form of guano by each species of adult penguin for each colony as the product of four parameters using the following equation:

$$Q=S\times T\times R\times C\times 10^{-9}, \qquad (1)$$

where S is the population size of penguins (individuals), T is the breeding time of penguins spent in Antarctica each year (d/a), R is the penguin excretion rate (g/d/individual, dry weight), and C is the phosphorus content of penguin guano (mg/kg, dry weight).

The population size of penguins (S) in the Ardley Island colony was measured using direct counting (Sun et al., 2010), but in the Vestfold Hills and on Ross Island the population size was estimated using aerial photographic survey (Whitehead and Johnstone, 1990; Ainley et al., 2004). The time the penguins spent in Antarctica each year (T) was determined by direct observation for all three colonies (Taylor, 1962; Puddicombe and Johnstone, 1988; Sun et al., 2010). The mean number of droppings per day was counted in the field, and guano was sampled then air-dried at room temperature to obtain the mean weight per dropping. The penguin excretion rate (R) was the product of the mean number of droppings per day and the mean weight per dropping. We assumed negligible error associated with all three parameters (S, T, and R) mentioned above.

Phosphorus content of penguin guano (C) was determined using inductively coupled plasma-optical emission spectroscopy (ICP-OES), and each sample was processed three times. Uncertainty estimates were based on the standard deviation of the phosphorus content in guano.

3 RESULT

Population size, breeding time, excretion rate, and phosphorus content, together with the estimated annual total amount of phosphorus transferred by penguins in the three study areas, are presented in Table 1. The population size of penguins (S in Eq.1) varied among different regions during the breeding season. A large number of penguins were observed in the Vestfold Hills colony (393 184 individuals) and the Ross Island colony (330 316 individuals), approximately 40-fold more than in the Ardley Island colony (9 704 individuals). The length of breeding time (T in Eq.1) varied little between Gentoo penguins and Adélie penguins because they belong to the same genus, *Pygoscelis*, and have similar breeding habits. The excretion rate (R in Eq.1) varies at different stages of the breeding cycle. More excreta are deposited during the chick feeding period than during the molt fast period (Lindeboom, 1984).

The phosphorus content (C in Eq.1) in the guano of different species of penguins in different areas varied dramatically, ranging from 22 911–102 861 mg/kg (Table 1). The composition of the guano of seabirds reflects their diet (Brimble et al., 2009), and the phosphorus level in penguin guano is linked to the

Table 1 Estimated annual amount of phosphorus transported by penguins from ocean to land

Location	Penguin species	Population (individual)	Breeding time (d/a)	Excretion rate (g/d/individual)	P content in guano (mg/kg) Mean±SD	Annual amount of P (kg/a) Mean±SD
Ardley Island	*P. papua*	8 858[a]	153[a] Oct.–Feb.	84.5[f, g]	102 816±3 089[h]	11 775±354
Ardley Island	*P. adeliae*	846[a]	132[a] Oct.–early Feb.	84.5[f, g]	60 821±1 904[i]	574±18
Vestfold Hills	*P. adeliae*	393 184[b]	182[d] Early Oct.–Mar.	84.5[f, g]	27 624±1 009[j]	167 036±6 101
Ross Island						
Cape Crozier	*P. adeliae*	240 719[c]	153[e] Oct.–Feb.	84.5[f, g]	22 911±547[h]	71 302±1 702
Cape Bird	*P. adeliae*	82 921[c]	153[e] Oct.–Feb.	84.5[f, g]	22 911±547[h]	24 561±586
Cape Royds	*P. adeliae*	6 676[c]	153[e] Oct.–Feb.	84.5[f, g]	22 911±547[h]	1 977±47
Total						277 226±8 808

Note: [a] Sun et al., 2010; [b] Whitehead and Johnstone, 1990; [c] Ainley et al., 2004; [d] Puddicombe and Johnstone, 1988; [e] Taylor, 1962; [f] Wu, 1998; [g] Sun and Xie, 2001; [h] This study; [i] Sun et al., 2006; [j] Huang et al., 2009.

Table 2 Proportion of Antarctic krill (*E. superba*) in the diet of penguins (wet weight)

Location	Penguin species	Proportion of krill (%)	References
Ardley Island	*P. papua*	86.87	Wu, 1998
Ardley Island	*P. adeliae*	81.79	Wu, 1998
Vestfold Hills	*P. adeliae*	45 (pre-hatching)–73 (post-hatching)	Green and Johnstone, 1988
Ross Island	*P. adeliae*	74 (crèche)–85 (guard)	Lyver et al., 2011

proportion of krill in their diet. For example, as shown in Table 2, the percentage of krill in the diet of Gentoo penguins (86.87%) is higher than in the diet of Adélie penguins (81.79%), probably a result of different feeding preferences of the two penguin species. This difference in diet composition is reflected in the content of phosphorus in the guano of Gentoo penguins (102 861 mg/kg) and Adélie penguins (60 821 mg/kg).

The content of phosphorus in Adélie penguin guano also varied among the three study areas. Adélie penguin guano contained 60 821 mg/kg phosphorus on Ardley Island, 27 624 mg/kg in the Vestfold Hills, and 22 911 mg/kg on Ross Island. This finding was also consistent with the variation in the proportion of krill in the penguin diets among the three sites (Table 2). The proportion of krill in the diet of the penguins appears to be the main factor affecting the phosphorus content in guano, and is closely associated with foraging behavior. For example, the foraging behavior of Adélie penguins is mainly affected by food availability (Lynnes et al., 2004). Krill are unevenly distributed in the Southern Ocean, with about 70% of the total population concentrated in the southwest Atlantic sector (Atkinson et al., 2004). They are found in reasonable numbers in the Ross Sea (Hill et al., 2006), but are not prevalent in the southern Indian Ocean sector (Pauly et al., 2000). The abundant supply of krill in the water around Ardley Island leads to a high proportion of krill in the penguins' diet, and to the high phosphorus content in the guano of penguins in this area.

4 DISCUSSION

4.1 Estimation of phosphorus transferred from ocean to land by penguins in Antarctica

In this study, we estimated the amount of phosphorus derived from adult penguins over their summer breeding time to be 12 349, 167 036, and 97 841 kg/a on Ardley Island, in the Vestfold Hills, and on Ross Island, respectively, with a total of 2.77×10^5 kg/a across our three study sites. The data for the three penguin populations were acquired during different years (Ardley Island in 2006–07, Vestfold Hills in 1981–82, and Ross Island in 1997–2000). However, because T, R, and C in Eq.1 are relatively consistent among the different penguin species and colonies (Table 1), the variation among the three sites is primarily a result of variation in penguin population size (S).

At the Ardley Island colony, in the maritime Antarctic, the input of phosphorus from physical transport and atmospheric deposition was 23.80–732.38 kg and 8.78 kg, respectively (Qin et al., 2013). The amount of phosphorus transported by penguins to

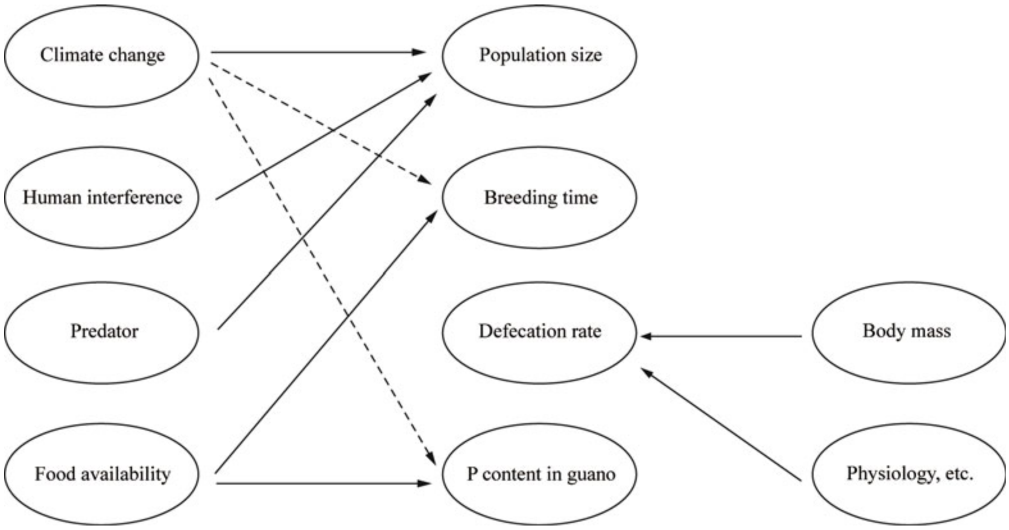

Fig.1 Factors influencing the amount of phosphorus transferred by penguins

this island was 12 349 kg, highlighting the importance of the role of penguins in transporting phosphorus. Worldwide, the phosphorus transferred from sea to land in seabird guano is 1.0×10^{7}–1.0×10^{8} kg/a (Polis et al., 1997), 0.28%–2.77% of which can be accounted for by the phosphorus transferred by Antarctic penguins in our three study areas. Furthermore, according to the content of phosphate (0.55–2.26 μmol/L) in seawater of Pruz Bay (Han et al., 2010), the total amount of phosphorus transferred by penguins in our study equivalent to an annual input of 3.96×10^{9}–1.63×10^{10} kg seawater to land of Antarctica.

Previous studies have shown that the amount of nutrients transported by biological vectors has significant temporal and spatial variation. For example, the amount of penguin guano transported to land in the Admiralty Bay area has rapidly fallen to one third of the amount (230 kg) recorded in the 1970s (Rakusa-Suszczewski, 2003), which can be attributed to a significant decline in local penguin populations and snow precipitation (Nędzarek, 2010). Many other factors may also impact on the amount of nutrients transferred by penguins. As shown in Fig.1, climate change (Sun et al., 2000), human disturbance (Trivelpiece et al., 2011), and predators (Pitman and Durban, 2010) all affect penguin population size (S in Eq.1). Climate change (Barbraud and Weimerskirch, 2006) and food supply (Taylor, 1962) can affect breeding time (T in Eq.1), and excretion rate (R in Eq.1) may be linked to animal body mass, physiology, and food energy (Hahn et al., 2007). Climate change, which affects the relative abundance of fish and squid in the diet of Adélie penguins (Emslie et al., 1998), and food availability (Brimble et al., 2009) will also affect the phosphorus content in penguin guano (C in Eq.1). Therefore, climate change, human disturbance, and food availability all influence the four parameters in Eq. 1, in turn affecting the amount of phosphorus transferred by penguins.

4.2 Impacts of phosphorus transferred from ocean to land on ice-free areas in Antarctica

Antarctica is cold and infertile, and nutrients transferred from sea to land by penguins are crucial in supporting the ecosystems of ice-free areas on the Antarctic continent. The phosphorus concentration of soils in penguin breeding colonies is higher than in non-breeding colonies (Tatur and Myrcha, 1984). Furthermore, the total amount of phosphorus in soils and mosses in areas colonized by penguins in Edmonson Point, northern Victoria Land, was higher compared with two other sites. This was attributed in part to the dissolution of high phosphorus concentrations in penguin guano (Bargagli et al., 1998). Besides fertilizing plants, phosphorus from penguin guano can be transported into lakes and streams, influencing the water chemistry and phytoplankton growth. In a study of Boeckella Lake at Hope Bay in the Antarctic Peninsula, Izaguirre et al. (1993) found the highest phosphorus concentrations, phytoplankton densities (Chlorophyceae and Cyanophyceae), and mean species richness in the lake areas downstream from the base of penguin rookeries. In contrast, the water unaffected by penguins had very low total phosphorus and mean species richness (Izaguirre et al., 1993). Similar results were found in the water bodies around the Henryk Arctowski Polish

Antarctic Station on King George Island (Nędzarek and Pociecha, 2010). In that study, the authors also discussed how the varying impacts of penguin rookeries might contribute to different nutrient conditions. In addition, Huang et al. (2011) identified phosphorus as the optimal bio-element in Adélie penguin guano, and found that phosphorus was obviously enriched in sediment from penguin rookeries. Phosphorus from penguin guano therefore greatly influences the terrestrial and freshwater ecosystems of Antarctica.

5 CONCLUSION

In this paper, we estimated that the amount of phosphorus transferred in penguin guano in three colonies was 2.77×10^{5} kg during their annual breeding season, equivalent to an input of 3.96×10^{9}–1.63×10^{10} kg of seawater to the land of Antarctica. Our study showed that seabirds, such as penguins, transfer not only contaminants but also nutrients from the ocean to land, and play an important role in sustaining the diversity of unproductive terrestrial ecosystems in Antarctica. This paper also provides a typical reference method for estimating the amount of nutrients transferred between sea and land, or between fresh water and land interfaces.

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