Latitudinal range shifts in Australian flying-foxes: A re-evaluation

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Abstract Recent range shifts towards higher latitudes have been reported for many animals and plants in the northern hemisphere, and are commonly attributed to changes in climate. Relatively little is known about such changes in the southern hemisphere, although it has been suggested that latitudinal distributions of the fruit-bats Pteropus alecto and Pteropus poliocephalus changed during the 20th century in response to climate change in eastern Australia. However, historical changes in these species distributions have not been examined systematically. In this study we obtained historical locality records from a wide range of sources (including banding and museum records, government wildlife databases and unpublished records), and filtered them for reliability and spatial accuracy. The latitudinal distribution of each species was compared between eight time-periods (1843–1920, 1921–1950, five 10-year intervals between 1950 and 2000, and 2001–2007), using analyses of both the filtered point data (P alecto 870 records, P poliocephalus 2506) and presence/absence data within 50 × 50 km grid cells. The results do not support the hypothesis that either species range is shifting in a manner driven by climate change. First, neither the northern or southern range limits of P poliocephalus (Mackay, Queensland and Melbourne, Victoria respectively) changed over time. Second, P alecto’s range limit extended southward by 1168 km (approximately 10.5 degrees latitude) during the twentieth century (from approximately Rockhampton, Queensland to Sydney, New South Wales). Within this zone of southward expansion (25–29°S), the percentage of total records that were P alecto increased from 8% prior to 1950 to 49% in the early 2000s, and local count data showed that its abundance increased from several hundred to more than 10 000 individuals at specific roost sites, as range expansion progressed. Pteropus alecto expanded southward at about 100 km/decade, compared with the 10–26 km/decade rate of isotherm change, and analyses of historical weather data show that the species consequently moved into recently-colder regions than it had previously occupied. Neither climate change nor habitat change could provide simple explanations to explain P alecto’s observed rapid range shift. More generally, climate change should not be uncritically inferred as a primary driver of species range shifts without careful quantitative analyses.

Key words: climate change, fruit bat, geographical distribution, land-use change, urbanization.

INTRODUCTION

The study of the geographic distributions of species and the reasons why species occur where they do are fundamental themes in ecology (Krebs 2001). There is evidence of recent changes in the distributions of many species (Walther et al. 2002; Parmesan & Yohe 2003; Hickling et al. 2006), including plants (Grabherr et al. 1994; Sturm et al. 2001), birds (Thomas & Lennon 1999; Hockey & Midgley 2009) and butterflies (Parmesan 1996; Parmesan et al. 1999). Distributional change may occur in a variety of ways. However, the most commonly observed distributional shift consists of range expansion towards higher latitudes or higher elevations (Walther et al. 2002; Parmesan & Yohe 2003; Root et al. 2003). Habitat modification and climate change are thought to be the most common factors causing recent changes in distribution (Hughes 2000; Warren et al. 2001; Fahrig 2003), although other factors can also modify species distribution including translocations by humans, biotic interactions (e.g. competition, predation and mutualism) and hunting (Towns & Daugherty 1994; Davis et al. 1998; Root et al. 2003; Parmesan et al. 2005; Hockey & Midgley 2009).

In recent years, the emerging impacts of global climate change have increasingly been held responsible for changes in species distributions (Walther et al. 2002; Hughes 2003; Parmesan & Yohe 2003; Root et al. 2003). These concerns have stimulated renewed interest in the influence of climatic variables on the range limits of species. However, there are two risks associated with attributing observed changes in species
distributions to climate change. First, the occurrence of range shifts may be prematurely inferred from limited data. Second, observed changes in species distributions may be attributed to climate change without adequate scrutiny of alternative factors.

Demonstrating that distributional shifts have occurred or are occurring requires statistically robust quantitative comparisons of historical and present data. Although there are good examples of such studies in the northern hemisphere (Walterh et al. 2002; Parmesan & Yohe 2003; Root et al. 2003), there are few well-documented examples of latitudinal shifts for Australian terrestrial species. It has been suggested that the southern range limit of the Black Flying-fox (Pteropus alecto) in Australia has extended southward during the past century (Eby et al. 1999; Tidemann 1999; Hall & Richards 2000; van Dyck & Strahan 2008), and that both the northern and southern range limits of the Grey-headed Flying-fox (Pteropus poliocephalus) have also shifted southwards (Tidemann 1999; van der Ree et al. 2006; van Dyck & Strahan 2008). These changes in distribution were initially attributed to climate change by Tidemann (1999). Although untested, this idea has been propagated by subsequent authors (Tidemann & Nelson 2004; van der Ree et al. 2006; Wellbergen et al. 2007; van Dyck & Strahan 2008), cited as evidence supporting climate-change impacts (Hughes 2003), and repeatedly quoted in public statements as a local exemplar of such impacts.

In the present study we undertake a quantitative analysis of historical and present distributions of P. alecto and P. poliocephalus in eastern Australia. The results are used to evaluate the robustness of previously published inferences concerning distributional shifts in these species, and the evidence that global warming has been a driver of these shifts.

**METHODS**

**The species and their distributions**

*Pteropus alecto* is widespread in coastal subtropical and tropical northern and eastern Australia (Hall & Richards 2000; Churchill 2008). It is also found in parts of southern New Guinea, and the Indonesian islands of Sumba, Lombok and Celebes (van Dyck & Strahan 2008). In northern Australia, *P. alecto* has been found as far as 250 km inland (Thompson 1991), but typically occurs in coastal areas (Hall & Richards 2000). Since the 1930s, *P. alecto* is reported as expanding its southern range limit from Maryborough (25.5°S) to Sydney (33.9°S), and this southward shift has been described as being particularly rapid since 1990 (Tidemann 1999; van Dyck & Strahan 2008; DECCW 2009).

*Pteropus poliocephalus* is endemic to coastal eastern Australia, at mainly subtropical and temperate latitudes (Tidemann 1999; van Dyck & Strahan 2008). The current distribution of *P. poliocephalus* is reported as extending from around Maryborough (25.5°S) to Melbourne (37.8°S) (Tidemann 1999; van Dyck & Strahan 2008). The inland boundary is difficult to define but typically this species occurs from the coast to at least the Great Escarpment throughout the species range and as far inland as the tablelands and western slopes of the Great Diving Range in northern New South Wales and southern Queensland (van Dyck & Strahan 2008; DECCW 2009). It has been suggested that the northern range limit of *P. poliocephalus* has contracted by up to 750 km over the past 100 years (Tidemann 1999; van Dyck & Strahan 2008).

In regions where the distributions of the two species overlap, they share day time roosts and night time foraging habitat. Roost sites (camps) typically comprise between hundreds and thousands of individuals and occur in dense, riparian or wetland forests including rainforests, *Melaleuca* forests, and mangroves (Eby 1991; Tidemann 1999; Hall & Richards 2000; Roberts 2005). Camps can be used on a seasonal or continuous basis, and numbers of bats within a camp can fluctuate widely, associated with variation in surrounding flower and fruit resources (Eby 1991; Tidemann 1999; Hall & Richards 2000). Both species are very mobile. Long-distance movements of over 600 km in *P. alecto* (A. Breed, pers. comm., 2010) and over 800 km in *P. poliocephalus* (Tidemann & Nelson 2004) have been recorded during a time-period of 1 month. Within a typical night’s foraging, species commonly travel up to 20 km from the roost (Eby 1991; Palmer & Woinarski 1999; Tidemann 1999; Markus & Hall 2004), often across cleared and fragmented landscapes.

**Construction of distributional database**

All available locality information for *P. alecto* and *P. poliocephalus* in eastern Australia were collated, from the time of early European exploration to December 2007. The study area extended from the northern to the southern extremities of the mainland, and 250 km inland to include the western slopes of the Great Diving Range. The resulting database contained information on the species (*P. alecto* or *P. poliocephalus*), date, latitude, longitude, name or description of locality, source of the record, observed behaviour (roosting, foraging or unspeciﬁed), and any information on numbers of individuals present (if available).


The data were then filtered as follows. Records were deleted if they lacked information on location (latitude and longitude or location description), year or species. Repeated sightings at the same location in the same year were collapsed into one record per location per year per species. Records considered to be ‘vagrants’, defined as roost locations with
less than 10 individuals were also deleted (n = 22). However, most records did not include information on the number of individuals present and may include vagrant sightings. A randomly selected subset (10%) of museum specimens, together with all museum specimens collected at the two species northern and southern range boundaries, were re-examined either by the museum curator or B. Roberts to determine whether the species had been correctly identified. Some erroneous early records at or near range limits were consequently removed (see Roberts et al. 2008). But recent museum records were found to be reliable.

All non-museum records were also screened for reliability. For example, data compiled in state government wildlife atlases contained information from a range of sources including published literature, environmental consultants' reports and other 'grey' literature, unpublished field surveys and incidental observations. To ensure that the analysed data were reliable, records were only retained if an observer was named, and if this person was considered to have the expertise needed to identify flying-foxes to species level (e.g. long-term naturalists, researchers, wildlife carers and experienced government staff); observers' levels of expertise were assessed through consultation with experts familiar with the experience of individual collectors.

To screen for spatial accuracy, the data were imported into ArcView (Version 3.3) and overlaid with geographical landmarks and bioregional boundaries to identify localities that were obviously outliers. Records (n = 26) that were obviously erroneous (i.e. in the ocean or that were >500 km outside likely range boundaries) were removed. At the conclusion of the screening process, 3376 records (P. alecto 870, P. poliocephalus 2506; Appendix S1) remained and this dataset is referred to as 'point records'. For analyses, the point records were grouped in two ways, into either eight time-periods: 1843–1920, 1921–1950, 1951–1960, 1961–1970, 1971–1980, 1981–1990, 1991–2000 or 2001–2007, and four time-periods: 1843–1950, 1951–1990, 1991–2000 and 2001–2007.

Observation effort varied spatially and temporally. To reduce consequent biases in the data, point records were converted to presence/absence records within 50 × 50 km grid cells. The scale was chosen to encompass the maximum known nightly foraging distances of P. alecto and P. poliocephalus (Eby 1991; Tidemann 1999; Markus & Hall 2004). A grid lattice covering the study area was investigated in ArcView (Version 3.3), with grid cells defined by their centre points. Each cell of the lattice was interrogated for presence of point records of each species within each of the eight time-periods, yielding 222 ‘grid records’ for P. alecto and 368 for P. poliocephalus.

**Distributional changes in Pteropus alecto and Pteropus poliocephalus**

Box plots were constructed from both the point records and grid records to describe the latitudinal distribution of each species across time. Whether the distribution of each species had expanded or contracted in a north-south distance over time was assessed by calculating Spearman rank correlation coefficients between time-periods (ranked) using each of five distributional variables: the median, minimum, maximum and upper and lower 25% quartiles of the species latitudinal occurrence.

To investigate changes through time in the proportion of each species across eastern Australia, the percentages of point records attributed to P. poliocephalus in six uniform latitudinal bands (10°–14°, 15°–19°, 20°–24°, 25°–29°, 30°–34°, 35°–39°S) were graphically compared among the four time-periods.

**Analysis of climate within range of Pteropus alecto**

The influence of climate on the southern limit of P. alecto was investigated using temperature and rainfall data obtained from the Australian Bureau of Meteorology (BOM 2010). We selected weather stations corresponding to each of four spatio-temporal options: the latitudes of lower quartile and most southern limit of grid records in both the 1921–1950 and 2001–2007 time-periods. Suitable weather stations were sought on the basis of the following criteria: located within 1 degree of latitude (100 km) of the central point of the relevant grid cell, elevation <20 m and located within 30 km of the coast. Only one weather station at each of the four latitudinal locations met all these criteria: 1921–1950 lower quartile – St Lawrence (22.35°S, 149.43°E), 1921–1950 southern limit – Maryborough (25.52°S, 152.72°E), 2001–2007 lower quartile – Archerfield Airport (Brisbane) (27.57°S, 153.01°E) and 2001–2007 southern limit – Sydney Airport (33.86°S, 151.21°E). Climatic variables considered were: annual mean minimum and maximum temperatures, annual rainfall and mean annual number of days <2°C (frost potential). A complete set of data was available across all four weather stations from 1939 to 1949, and data from this period were therefore used to indicate climate in 1921–1950 (weather data were incomplete at many stations prior to 1939 and in 1950).

**Trends in the abundance of flying-foxes within specific camps**

Data on species abundances within specific flying-fox camps were compiled from available roost counts at locations within the latitudinal zone in which distributional change had been suggested in the literature (25°–34°S), and the time-period of transition as revealed through analysis in the present study (1950–2007). Only one camp, Currie Park (28.8°S, 153.3°E), had reliable long-term abundance data for both P. alecto and P. poliocephalus that were collected using the same counting technique (exit counts) in the same months of the year (April and July), with the earliest count year being 1988. Exit counts involve a team of observers stationed around the camp who count the numbers of flying-foxes as they depart at dusk to feed (Eby et al. 1999). Data for Currie Park were compiled from published and unpublished surveys over two time-periods: 1988–1990 (Eby & Palmer 1991; P. Eby, unpubl., 1990) and 1998–2004 (Eby 2002, 2003, 2004). Data were collected approximately monthly in 1988–1990 and during April and July in 1998–2004. The abundances of both species at Currie Park were compared between 1988–1990 (n = 3) and 1998–2004 (n = 6) using Mann–Whitney U-tests. Abundance in each year of data was the number of
each species recorded in exit counts for either April or July, or
the average of these months if both were available.

RESULTS

Number and distribution of observations

The earliest point record in the database was of a *P. poliocephalus* collected at Cape Upstart (19.8°S, 147.8°E) in 1843 (Dobson 1878; Andersen 1912). Over 41% of records of *P. alecto* and 27% of records of *P. poliocephalus* were from daytime roost sites (Appendix S1); only one record of *P. alecto* and five records of *P. poliocephalus* were at foraging locations; the remainder may have been from either roosting or foraging locations.

The 870 point records for *P. alecto* were spread from 10.8°S (the northern tip of Cape York) to 33.9°S (Sydney), while 2506 point records for *P. poliocephalus* ranged from 19.8°S (near Bowen) to 38.9°S (southernmost Victoria) (Fig. 1). Records for both species were concentrated around 27.5°S and 34°S, corresponding with the human population centres of Brisbane and Sydney. The number of records increased markedly in the 1991–2000 and 2001–2007 time-periods and there was a substantial increase in records of *P. alecto* in a restricted latitudinal zone between 27.4°S (Brisbane, Queensland) and 28.4°S (Muirwilmabh, New South Wales) during 2001–2007 (Fig. 2a). This was associated with a series of targeted surveys of flying-foxes during that time to document winter concentrations of *P. poliocephalus* in the region (e.g. Eby 2002), which also recorded *P. alecto*. This effect was eliminated by the conversion of data to grid records (Fig. 2b).

Distributional changes in *Pteropus alecto* and *Pteropus poliocephalus*

There was a significant correlation between time and the most southerly record of *P. alecto* from both point and grid records (Table 1). The southern limit of known records of *P. alecto* expanded southward between 1912 and 2007 by 1168 km or approximately 10.5 degrees (Fig. 2; Appendix S2). Prior to 1920, *P. alecto* was not recorded further south than 23°S (near Rockhampton) but by 2007 the species had been recorded at 34°S (in Sydney). Both the upper and lower quartiles of grid records for *P. alecto* also shifted southward over time (Fig. 2) in a statistically significant manner (Table 1). However, there was no significant shift in its northernmost limit (Table 1).

![Fig. 1. Locality (point) records for (a) *Pteropus alecto* (*n* = 870) and (b) *Pteropus poliocephalus* (*n* = 2,506) in coastal eastern Australia from 1843 to 2007. Eastern records were limited to within 250 km from the coastline. Place names: B, Brisbane; M, Melbourne; Mb, Maryborough; Mk, Mackay; R, Rockhampton; S, Sydney.](image_url)
Fig. 2. Box plots showing the latitudinal distribution of *Pteropus alecto* (upper; grey) and *Pteropus poliocephalus* (lower; white) in eastern Australia between 1843 and 2007 using (a) point records and (b) 50 × 50 km grid data. Unless otherwise stated the year label shows the mid-year of the time-period. Numbers above bars are sample sizes (number of records or number of grids).

Table 1. Correlations (Spearman rank, n = 8 time-periods) between parameters describing the latitudinal distribution of *Pteropus alecto* and *Pteropus poliocephalus* and time using point and grid records (see Fig. 2)

<table>
<thead>
<tr>
<th></th>
<th><em>P. alecto</em></th>
<th><em>P. poliocephalus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Point records</td>
<td>Grid records</td>
</tr>
<tr>
<td>Most northern record</td>
<td>−0.26</td>
<td>−0.41</td>
</tr>
<tr>
<td>Upper quartile</td>
<td>0.74*</td>
<td>0.77*</td>
</tr>
<tr>
<td>Median</td>
<td>0.52</td>
<td>0.25</td>
</tr>
<tr>
<td>Lower quartile</td>
<td>0.74*</td>
<td>0.81*</td>
</tr>
<tr>
<td>Most southern record</td>
<td>1.00**</td>
<td>0.99**</td>
</tr>
</tbody>
</table>

*P < 0.05; **P < 0.01
There were no significant changes in either the northern or southern range limits or distributional quartiles of *P. poliocephalus* (Table 1; Fig. 2; Appendix S3). There were records in every decade between 1880s and 2000s of *P. poliocephalus* from the southernmost latitudes of continental Australia. At the northern limit, records of *P. poliocephalus* south of 23°S (Rockhampton) were common and consistent through time, and records of *P. poliocephalus* north of 23°S were rare both in the earlier historical periods (1843–1950) and in recent decades (1990–2007). Only two historical records occurred north of 23°S. Each was collected in the late 1800s during scientific expeditions. *Pteropus poliocephalus* was not recorded again north of 23°S until the 1990s from a single sighting of large numbers at Eungella in 1991 together with repeat sightings between 2005 and 2007 from the nearby Finch Hatton camp (both west of Mackay; 20.9°S). Close scrutiny of historical records in the far north of the species range (north of 20.9°S) revealed that most were either questionable or incorrect (see also Roberts et al. 2008).

Vagrant records were re-introduced into the dataset to assess their impact on results. The only effect on latitudinal distribution was a southward shift of the most southern record of *P. alecto* in the 1981–1990 time-period by 2 degrees (28.4–30.6°S), resulting from a single observation; this did not affect the statistical relationships. Including vagrant sightings (*n* = 12) had no effect on the latitudinal distribution of *P. poliocephalus*.

In the zone of *P. alecto’s* southward expansion (25–29°S), the percentage of records that were *P. poliocephalus* declined significantly, from 92% (of 13 records) prior to 1950 to 51% (of 619 records) by the early 2000s (Fig. 3; test of association chi-squared = 8.682, *P* = 0.003, d.f. = 1).

**Climate dynamics at *Pteropus alecto*’s changing southern limits**

The mean annual maximum and minimum temperatures at locations representing *P. alecto*’s southern range limit in 1921–1950 (southernmost record and lower quartile) increased by 0–2.0°C between 1939–1949 and 2001–2007 (Table 2). However, the 2000–2007 temperatures at the new locations representing its southern limits (in 2000–2007) were substantially cooler than 1939–1949 temperatures at its 1921–1950 southern limits (effective decreases of 0.7–4.3°C in mean annual maximum and minimum temperatures, Table 2). Therefore, in spite of an overall pattern of warming over time at all locations, *P. alecto* experienced temperature decreases in the southern part of its distribution as a result of its range expansion. The limited available frost data (annual days <2°C) indicate that *P. alecto*’s lower distributional quartile in 2000–2007 includes frost-prone locations. Annual rainfall was generally lower in 2000–2007 than in 1939–1949, but did not vary consistently or meaningfully with latitude (Table 2).

**Abundance trends in the Currie Park camp**

The abundance of *P. alecto* during April and July increased significantly in the Currie Park roost between 1988–1990 and 1998–2004 (*U* = 0.0, *P* = 0.02: Fig. 4). Numbers of *P. poliocephalus* in 1988–1990 generally exceeded those during 1998–2004 (Fig. 4), but there was no significant difference in either the abundance of *P. poliocephalus* (*U* = 4.5, *P* = 0.24) or the total number of flying-foxes (*U* = 5.0, *P* = 0.30).
DISCUSSION

Species-specific range dynamics and their possible causes

This study has detected a clear range shift by *P. alecto*, in spite of the sampling variability and potential biases inherent in the use of data compiled from a variety of sources which include volunteer observers. Because *P. alecto* and *P. poliocephalus* commonly occur together and are morphologically and ecologically similar, the same biases would apply to both species. Therefore, the species differences in geographical range dynamics as revealed by the present study cannot be an artefact of sampling. From the late 1800s to 2007, *P. alecto* expanded its southern range boundary poleward by 123 km per decade on average. This rate is broadly similar to the poleward range-limit movement reported for some butterflies (up to 193 km/decade, Parmesan *et al.* 1999; Crozier 2004), but generally higher than observed for birds (9–20 km/decade, Thomas & Lennon 1999; Hickling *et al.* 2006). In cases where the southward movement of *P. alecto* into new areas has been observed at particular sites, there have been initial sightings of tens to hundreds of individuals, which were then followed by sometimes-rapid increases of up to tens of thousands (although the number varies greatly), such as documented here for Currie Park. There may be a time lag from when *P. alecto* first arrives in an area until it builds up to sufficient numbers to be noticed, because they typically roost together with *P. poliocephalus*.

There are two major environmental changes that have previously been used to explain the shifts in flying-fox distribution, climate change and habitat change. First, the poleward movement of *P. alecto* is superficially

Table 2. Differences in four climatic variables at four latitudinal locations representing the lower quartile and most southern limit of grid records of *Pteropus alecto* at two time-periods, 1921–1950 and 2001–2007

<table>
<thead>
<tr>
<th>Latitudinal locations</th>
<th>Approx. °S</th>
<th>Annual maximum temperature (°C)†</th>
<th>Annual minimum temperature (°C)†</th>
<th>Mean no. days &lt;2°C</th>
<th>Annual rainfall (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lower quartile</td>
<td>1921–1950</td>
<td>22</td>
<td>28.5</td>
<td>29.0</td>
<td>na‡</td>
</tr>
<tr>
<td></td>
<td>2001–2007</td>
<td>28</td>
<td>25.5</td>
<td>26.8</td>
<td>13.4</td>
</tr>
<tr>
<td>Effective difference</td>
<td></td>
<td>–1.7</td>
<td>–2.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Most southern record</td>
<td>1921–1950</td>
<td>26</td>
<td>27.3</td>
<td>27.3</td>
<td>15.3</td>
</tr>
<tr>
<td></td>
<td>2001–2007</td>
<td>34</td>
<td>21.6</td>
<td>23.0</td>
<td>12.6</td>
</tr>
<tr>
<td>Effective difference</td>
<td></td>
<td>–4.3</td>
<td>–0.7</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

†The annual daily maximum or minimum air temperature per year, averaged over all years for either 2001–2007 or 1939–1949. ‡Data not available. §St Lawrence, Queensland (22.35°S, 149.54°E). ††Archerfield Airport, Brisbane, Queensland (27.57°S, 153.01°E). ‡‡Maryborough, Queensland (25.52°S; 152.72°E). §§ Sydney Airport (33.86°S; 151.21°E). Climatic data from 1939 to 1949 represent the earlier period due to incomplete records pre-1939. Effective difference is the estimated temperature difference actually experienced by *P. alecto* as a consequence of changed distributional limits; with the relevant before and after temperatures highlighted in bold.

Fig. 4. Population estimates of *Pteropus alecto* and *Pteropus poliocephalus* in the Currie Park camp, Lismore, during two time-periods, January 1988–July 1990 and July 1998–April 2004. Data are from camp exit counts in specific months which varied among years. The x-axis tick marks show December in each year. Approximately 1000 *P. alecto* were first recorded in the Currie Park camp in January 1985 (L. Hall, unpubl., 1985).
consistent with climate change scenarios (Hughes 2003). Tidemann (1999) suggested that increases in average rainfall and temperatures in eastern Australia have favoured the southward shift in \textit{P. alecto}'s southern range limit, with a reduction in number of days with frosts being of particular importance. Neither the rainfall patterns reported here nor the more widely observed declining temporal rainfall trend in eastern Australia (CSIRO 2007) support a rainfall hypothesis. Australia's continental average temperature has increased by approximately 0.9°C since 1910 and 0.1–0.2°C per decade since 1950 (Collins 2000; Hughes 2003; CSIRO 2007), including areas where \textit{P. alecto}'s range has expanded. In general, a temperature increase of 0.1–0.2°C per decade would correspond with a latitudinal shift in isotherms of approximately 10–26 km/decade (Hughes 2000). In contrast, \textit{P. alecto}'s southward expansion rate has been much faster: about 100 km/decade.

Furthermore, our analyses show that \textit{P. alecto} has progressively established camps in new areas that are considerably cooler than experienced in its previous historical distribution. While a general trend toward warmer temperatures across Australia may have led to a reduction in frost frequency in some locations (Stone et al. 1996; CSIRO 2007), the occurrence of frost is strongly influenced by local topography, and \textit{P. alecto}'s range expansion has been confined to the coast where frost potential is low and has not changed greatly with time. The data presented here do not support the hypothesis of climate change as a primary driver of \textit{P. alecto}'s southward range expansion.

The second environmental factor suggested to explain shifts in flying-fox distribution is habitat change. A large proportion of eastern Australian forests and woodlands have been converted to agriculture and urban development during this study's time-frame, particularly affecting coastal lowlands and subcoastal river basins (Catterall & Kingston 1993; NLWRA 2001; DECC 2006). Coastal and subcoastal lowland rainforests, eucalypt and melaleuca communities, and heathlands are important to flying-foxes as foraging and roosting habitat (Eby 1995; Hall & Richards 2000; Roberts 2005). However, it would be expected that losses of these habitats would disadvantage both flying-fox species. There is evidence to suggest that \textit{P. alecto} is not only expanding into urban areas but also persisting and increasing in abundance within those areas (Eby & Palmer 1991; Eby et al. 1999; Eby 2004; Roberts 2005). However, it is also likely that the population density of \textit{P. poliocephalus} is increasing in urban areas (Hall 2002; van der Ree et al. 2006). Therefore, current evidence does not suggest a mechanism whereby habitat change could have caused the combined range expansion of \textit{P. alecto} and relative range-stability in \textit{P. poliocephalus}.

Despite previous repeated claims in the literature (Tidemann 1999; van der Ree et al. 2006; van Dyck & Strahan 2008), there is no evidence for a progressive contraction of the northern range limit of \textit{P. poliocephalus}. Field surveys and satellite telemetry since 2007 also confirm that this species has continued to regularly use the far northern part of its distribution (Roberts et al. 2008). This negates suggestions that putative changes in the distribution of \textit{P. poliocephalus} provide support for the impacts of climate change on Australian wildlife (Tidemann 1999; Hughes 2003). Furthermore, such a change in the northern range boundary would not necessarily be expected if high temperatures are not a limiting factor. Between 1921 and 1990, the northern range limit of \textit{P. poliocephalus} appears to have temporarily shifted southward (by 5 degrees latitude; Fig. 2). This apparent contraction is consistent with the observation that many species show temporary spatial fluctuations in distributions at their range limits (Ayres & Lombardero 2000; Gaston 2003), or may simply be due to the random effect of low survey effort in this region during 1921–1990.

The abundance of \textit{P. poliocephalus} near its southern range limit in urban Melbourne has recently increased, accompanied by a change in its temporal pattern of occurrence from inconsistent to continuous, in spite of disturbance actions to relocate a large camp from the Royal Botanical Gardens (van der Ree et al. 2006). The southern limit of \textit{P. poliocephalus} has previously been described as having recently extended southwards into urban Melbourne because of the influences of climate change, increased food availability within the urban landscape and loss of habitat elsewhere (Parris & Hazell 2005; van der Ree et al. 2006; Williams et al. 2006). However, that view has been contested (DECCW 2009). Our results do not support the inference of a southerly range extension for this species, as it was first recorded in the Melbourne area in 1869 and was consistently present in every following time-period (Fig. 2). Nonetheless, a combination of increased food in urban Melbourne and habitat reduction elsewhere may have supported an increase in abundance.

In the north, \textit{P. alecto} records attenuate towards the Cape York Peninsula, even though this species range extends into New Guinea and Indonesia. In this zone of attenuation (16–19°S), a third species, the spectacled flying-fox \textit{Pteropus conspicillatus} occurs. These two species are ecologically and morphologically similar and their genetic status is unresolved (Webb & Tidemann 1995), and in this region they typically have not been recorded at the same roost sites (Churchill 2008). \textit{Pteropus alecto}'s northward range attenuation has increased over time, which may indicate a change in underlying distribution, or perhaps reflects the limited survey effort conducted in remote northern Australia, or alternatively a decrease in observers’ tendencies to
identify ambiguous individuals as *P. alecto* rather than *P. conspicillatus*.

**Interactions between the species**

A further possible factor affecting species range shifts is that of competition between ecologically similar species. Expansions to the southern limit of *P. alecto* have increased the area in which its distribution overlaps with that of *P. poliocephalus*. The mean weight of *P. alecto* is 674 g and that of *P. poliocephalus* is 782 g (Churchill 2008). In their zone of sympathy the two species are very similar in reproductive biology and seasonality (Eby 1995; van Dyck & Strahan 2008), diet and feeding ecology (McWilliam 1986; Eby 1991; Parry-Jones & Augee 1992; Eby 1995; Markus & Hall 2004), and roosting habitat (Tidemann 1999; Hall & Richards 2000). They are often found at the same roost sites (Hall & Richards 2000), although commonly partition space within the roost (Nelson 1965; Welbergen 2004; Roberts 2005).

The species appear to differ in their regularity of long distance movements, even though both are capable of rapid long-distance migrations. Distances of over 1000 km in a year are not uncommon for *P. poliocephalus* (Eby 1996; Tidemann & Nelson 2004; B. Roberts *et al.*, unpubl. data, 2009), whereas *P. alecto* tends to make long trips less frequently (Palmer & Woinarski 1999; Breed *et al*. 2010). Further, where mixed-species camps occur in the zone of sympathy, *P. alecto* tends to maintain small populations throughout the year, including times when *P. poliocephalus* have migrated elsewhere (P. Eby, pers. obs., 1989–2010). These different movement patterns may be driven by unknown ecological or behavioural differences, which may reduce the potential for competition.

Nevertheless, given their known similarities, it is likely that these species compete for some resources (Eby *et al*. 1999). For example, if *P. alecto* is a superior competitor, it could displace *P. poliocephalus* from food or roost resources (Tidemann 1999) as it moves southwards. Alternatively, *P. alecto* may be the inferior competitor and its recent expansion may be in response to past declines in the population of *P. poliocephalus* (e.g. those caused by hunting or habitat loss). However, there is no current evidence that *P. alecto* or *P. poliocephalus* use agonistic behaviours to complete directly for resources (DECCW 2009), but indirect forms of competition may also occur.

The abundance data presented here consistently suggest *P. poliocephalus* have declined within the area of distributional change since the arrival of *P. alecto*, although these results are not conclusive. Limited long-term data on the abundance of flying-foxes, and naturally high temporal variability in camp populations associated with the mobility and seasonal north-south migrations of *P. poliocephalus* (Eby 1991), make it difficult to verify long-term change. To clarify these issues requires further information, including better monitoring data at a range of sites in the geographic zone where *P. alecto* has expanded, and more information on the comparative ecology of the two species.

**CONCLUSIONS**

An important implication of this study’s results is that more careful quantitative analyses are needed to support inferences concerning austral species range shifts in response to climate change. For example, poleward extensions have recently been claimed in the distributions of Australian bird species, and these have been interpreted as consistent with effects of climate change (Olsen *et al*. 2003; Chambers *et al*. 2005; Olsen 2007), yet these range extensions have not been confirmed by statistical analyses. While it is indeed possible that climate-induced latitudinal range shifts are occurring in a number of Australian species, it is important that distributional data are analysed systematically to verify such shifts before inferences are made.

This study’s data analyses do not support the previous claim that recent climatic patterns have driven changes in the geographical distributions of *P. alecto* and *P. poliocephalus*. However, alternative processes of habitat change and interspecific interaction have also been insufficient to explain the two species observed contrasting patterns of temporal change, at least based on current knowledge. Further research is required to understand the causes of the recent rapid distributional change in *P. alecto* and the implications for its potential interaction with *P. poliocephalus*.

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REFERENCES


SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Data sources, time-period of records and number of records of Pteropus alecto and Pteropus poliocephalus.

Appendix S2. Grid records of Pteropus alecto.

Appendix S3. Grid records of Pteropus poliocephalus.