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Large-scale bird-movement patterns evident in eastern Australian atlas data

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Abstract. *Ad hoc* studies of the compositions of bird communities at dispersed sites and bird-banding data have failed to reveal the timing, destinations and movement patterns of most Australian migratory bird species. The analysis of national atlas and count data, on the other hand, has the potential to provide information on the species undertaking migratory movements, the timing of these movements, and their sources and destinations. This study examines atlas data of 407 species for evidence of movements by these species in eastern Australia.

Atlas and bird-count data were brought together to form the most extensive collection of bird observations in Australia. Mathematical, statistical and graphical tools were used to examine these data for evidence of temporal changes in the spatial distributions of each species. Examples are provided of the application of these tools to four speices (Dollarbird, *Eurystomus orientalis*, Noisy Miner, *Manorina melanocephala*, Grey Fantail, *Rhipidura fuliginosa* and the Budgerigar, *Melopsittacus undulatus*) that exhibit varying movement patterns.

A standardised analysis applying these indicators across 407 species found strong evidence of migratory movements for 101 of these species and suggestive evidence for a further 45 species. These results indicated 19 distinctive patterns of migration among the birds of eastern Australia.

Introduction

Very little is known about the large-scale movements of Australian land birds. However, understanding the nature of their movements is imperative to understanding their ecology and thus their conservation (Myers *et al.* 1987). Unfortunately, much recent ornithological research in Australia has been biased towards sedentary species (Clarke 1997). While many studies have described the patterns of movements of one or a few species, there is little information about the general patterns of large-scale bird movements in Australia.

The ecological significance of seasonal movements by Australian honeyeaters was examined by Keast (1968). He reviewed the limited evidence of movements in the literature at the time, as well as adding his personal observations, for 58 species. From this, Keast (1968) postulated very broad associations between movements and their timings, the areas in which they occur, and a short list of ecological factors assumed to influence these movements. Rowley (1975) classified 97 Australian migratory birds into three groups by the region in which their migration occurred. He also listed 46 species he suspected as being nomadic, to which he further added most of Australia's 69 honeyeaters, which he stated were nomadic for at least some part of the year. Consequently, well over 100 species (excluding seabirds and shorebirds) were suspected of undertaking long-distance movements. Neither Keast (1968) nor Rowley (1975) produced maps of movements such that their overall patterns could be examined.

Nix (1976) approached the movement patterns of birds from an ecological perspective. He examined well defined ecological factors and estimated how these would affect the movements of various trophic groups of birds (herbivore, insectivore, nectarivore, frugivore and graminivore). Unlike the studies of Keast (1968) and Rowley (1975), Nix's (1976) research produced a map of predicted seasonal movement patterns of Australian birds (Fig. 1). For eastern Australia, Nix (1976) predicted principally north–south migrations along the east coast and throughout the tropical regions. More localised are the east–west migratory routes predicted for the Murray River district of South Australia and Victoria, and from the Great Dividing Range and to the coast and inland areas. Within the arid interior of the country, Nix forecast 'essentially random movements (in response to episodic rainfalls) but with an underlying north–south bias which reflects the action of tropical and temperate weather systems at opposing seasons'.

Nix (1976) hoped that eventually bird-banding data would provide detailed insights into migratory patterns of many Australian species (as it has done in the Northern Hemisphere, e.g. Alerstam 1990), and with this, the testing of his predictions. However, in Australia the list of species for which patterns can be derived from band recoveries is

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extremely short as few recoveries of banded birds are made. Fullagar *et al.* (1986) listed 29 species for which banding data provided evidence of movements or, in some cases, lack thereof. Of these, sufficient recoveries were available for only four species (Silvereye, *Zosterops lateralis*, Australian Shelduck, *Tadorna tadornoides*, Cattle Egret, *Ardeola ibis*, and Pied Imperial Pigeon, *Ducula bicolor*) to produce maps from which large-scale patterns of movement could be inferred. While these patterns did compare favourably with the patterns predicted by Nix (1976), the quantity of bird-banding information available that Nix hoped for has failed to materialise. Fullagar *et al.* (1986) argued that Australia's vast size and small population is the reason for this problem. These limitations are unlikely to change, given the current levels of banding of migratory land birds. Baker *et al.* (1995) listed all long-distance bird-band recoveries in Australia during 1994–95. Most of this list comprised seabirds, with only seven recoveries across four land-bird species having their long-distance movements (100 km or more) observed directly. While bird-band recovery data can offer high-quality long-distance movement information, this data source is inadequate for investigating both the spatial and temporal patterns of migrations of Australian land-birds.

Other approaches like the use of Emlen Funnels are applicable to only a handful of species (e.g. Munro *et al.* 1993). Local or even regional studies of seasonal changes in the composition of bird communities (e.g. Pyke and Recher 1988; Osborne and Green 1992; Mac Nally 1995; Bentley and Catterall 1997) are inadequate if one's goal is to discern temporal and spatial changes in the distribution of a species throughout its range. At best one may be able to discern arrival and departure dates from such studies of small areas, but the sources or destinations of the birds in the area remain a mystery. Consequently, lists of mobile (as opposed to purely sedentary species) can be compiled (e.g. Chan 2001), but the spatial and temporal patterns of the movements of such species remain poorly understood. Clearly, new approaches for studying bird movements are required.

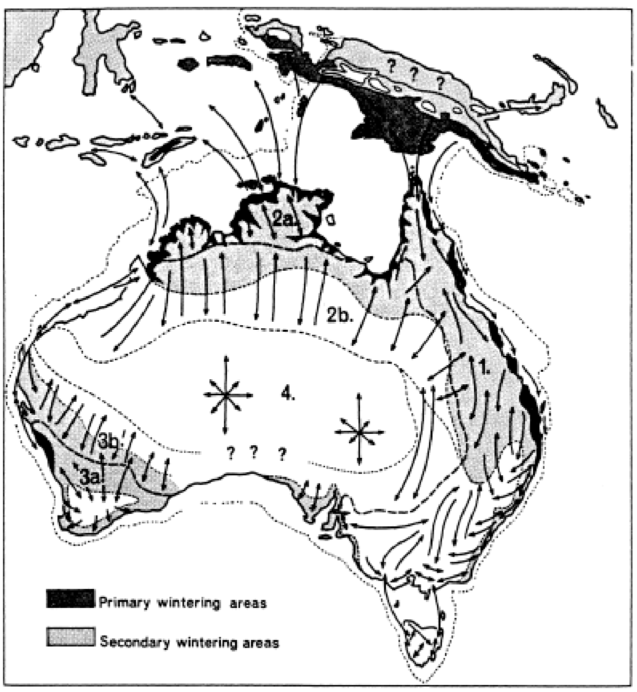


Fig. 1. Predicted over-wintering areas and seasonal movements patterns of Australian birds (reproduced with permission from Nix 1976).

Harrison (1991) demonstrated the utility of large national bird atlas data sets in the study of migratory bird patterns. He mapped the obvious seasonal variation in the distribution of the European Bee-Eater, *Meriops apiaster*, using the 'Atlas of Southern African Birds' data. Underhill *et al.* (1992) investigated the use of these atlas data to determine arrival and departure times of six migrants that breed outside southern Africa. These two movement studies were precursors to the detailed analysis of temporal changes in species' distributions in the 'Atlas of Southern African Birds' (Harrison 1995).

The South African studies demonstrated the potential for atlas-type data to describe the timing and patterns of movements of at least some species. Unfortunately, the past studies utilising these types of data (Underhill *et al.* 1992; Maurer and Heywood 1993; Harrison 1995; Villard and Maurer 1996; Hockey 2000) did not develop a generalised system of analysis tools.

Australia is in the fortunate position of having several similar national databases collected by volunteers describing the temporal distributions of our avifauna. These vast ornithological data sets have generally been under-utilised and analysed in isolation. However, if these data were combined, the resulting database would have enormous potential for extracting bird-movement information. Thus, the aims of this study were to address the following questions: How can atlas and count data be used to detect large-scale movements of Australian bird species? Which species undertake large-scale movements in Australia? What are the movement patterns of these species? Which species appear to have similar patterns? And, are these patterns similar to those proposed by Nix (1976)?

Methods

The methods presented to address these questions may be summarised as follows: Firstly, extensive data were brought together to describe temporal bird distributions across eastern Australia. Movement-indication statistics were then developed to detect and describe large-scale movements of species. The application of these tools is demonstrated using four sample species. A standardised combination of indicators was then used to classify species movements and, finally, these indicators were used to create generalised maps of movement patterns.

The 'Eastcoast' database

Bird atlas data were brought together from the sources listed in Table 1. The databases were combined as if all surveys were conducted within one theoretical year. Surveys of large areas (e.g. 2° latitude and longitude) or extended periods (>3 months) were not used. All surveys with

Table 1. The bird survey databases available to this study

This table lists the source database and the number of observers, surveys and observations within them. Detailed descriptions of each databases are given in the publications cited. Note that the New Atlas of Australia, the Canberra Ornithologists Group (COG) and the NSW Bird Atlas (NSWBA) projects are ongoing at the time of writing

Source (data time span)	Observers	No. of surveys	No. of observations	Reference
Historical Atlas (1950–76)	1265	113039	864522	Blakers *et al.* 1984
Field Atlas (1976–81)	1575	89640	2806881	Blakers *et al.* 1984
NSWBA (1982–97)	653	34453	1332589	Cooper and McAllan 1995
COG (1986–94)	395	11596	228365	Taylor and COG 1992
ABC (1989–95)	1052	78383	794728	Clarke *et al.* 1999
New Atlas (1998–2000)	2299	60317	1137237	Barrett 2000

three or fewer observations were excluded. The Australian Bird Count data were converted to presence/absence data to conform with the other databases. Care was taken to remove survey results that were duplicated across more than one database. Extensive data verification processes were employed in an attempt to remove erroneous sightings, dates and positions (Griffioen 2001).

Relatively few surveys in the combined database were conducted in the east and north of Western Australia and throughout outback Northern Territory and South Australia. Unfortunately, this paucity of data from these regions prohibited detailed temporal analyses of these areas. Therefore our analysis was restricted to the eastern half of Australia. The resulting combined database was called the 'Eastcoast' database (Fig. 2).

The Eastcoast database contained 4998207 observations of 755 species made in 187316 surveys at 37343 locations in eastern Australia. When considering the variation in the survey effort across different survey campaigns, it must be remembered that all the analyses presented are based on comparing reporting rates between periods of the year, but never between years. A reporting rate is defined as the number of times a species was detected as a proportion of the number of surveys performed within a grid-square during a particular period of the year.

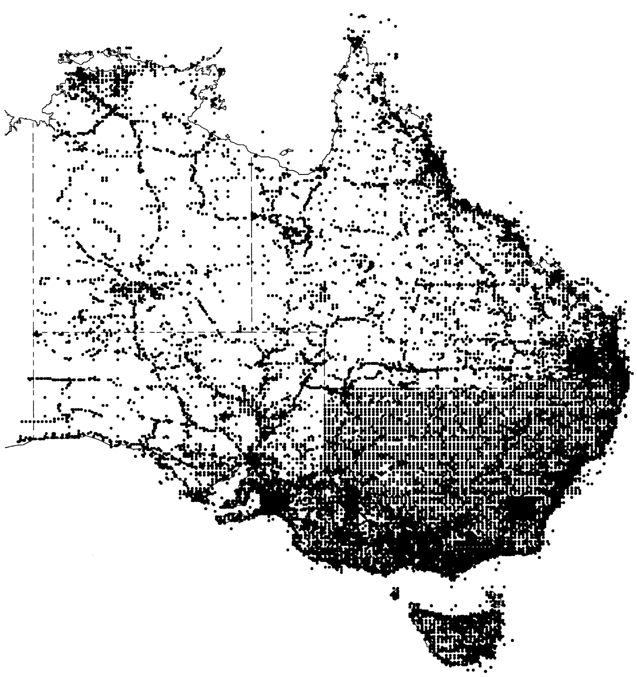


Fig. 2. Map of the survey sites in the 'Eastcoast' database.

Often hundreds of surveys were used to calculate the reporting rate for a single grid-square. Consequently, the influence of a single survey upon subsequent analyses was usually very small, further reducing the biases that might result from varying survey effort across the different survey campaigns. Furthermore, there is no reason to believe that the varied efforts expended in collecting these data would be systematically biased in any particular region within the eastern half of Australia.

Breeding season

The mid-point of the breeding season of each species provides a temporal reference point as to when that species is most likely to be at its breeding grounds and least likely to be moving. The Birds Australia Nest Record Scheme database was used to estimate the mid-point of the breeding season of each species. The details of these calculations are given in Griffioen (2001). Species without sufficient nest records to calculate a single mid-nest date were assigned the mean of all species' mid-nest dates (16 November). Note that the actual date is not critical to the success or failure of this study, as most calculations performed had a only three-month (quarter-year) temporal resolution. For each species, a three-month 'breeding' quarter was centred on the estimate of mid-point of the breeding season for that species. The three other quarters of the year, labelled the 'post-breeding', 'over-wintering' and 'pre-breeding' quarters, respectively, were derived by applying the respective three-month (91 days approximately) offsets relative to the average breeding date. Note that these terms are not intended to imply that breeding of each species occurs only during the breeding quarter, and that 'over-wintering' occurs during the winter months, but are used simply to indicate which quarter is being referred to, as the mid-point of the breeding season varies for each species.

Spatial resolution of statistical data

For each of the mathematical indicators presented, eastern Australia was subdivided into 200 km by 200 km grid-squares based on Zone 54 Australian Map Grid coordinates. For each grid-square in each quarter of the year, reporting rates were calculated only where at least five surveys occurred during the quarter within the grid-square. In order to appropriately weight coastal grid-squares, the ratio of landfall to grid-square area was multiplied by the reporting rate for the grid-square to correct the pseudo-population estimate (reporting rate multiplied by area) of each grid-square. This prevents overestimation of the pseudo-population sizes of the coastal grid-squares.

Movement-indication statistics

Spatial Distribution Test

Syrjala (1996) provides a Spatial Distribution Test that can be used to compare the spatial distribution of two populations, sub-groups within a population, or the same population at different times. It utilises a randomisation test to determine the likelihood of such differences between two distributions arising by chance. For this study, 10 000 randomisations were performed to model the change in the distribution of each species' 200-km grid-square reporting rates. The mathematical details of Syrjala's test are given in Syrjala (1996) and Griffioen (2001).

Movement Participation Rate

The 200-km grid-square quarterly reporting rates of each species provide an imprecise distribution map of the species for the quarter. If the sum of these values is assumed to represent the total population size for the study region for the quarter, then the redistribution of these values between quarters can provide an indicator of the minimum proportion of the population that must be moving between regions. This 'Movement Participation Rate' is similar to the migrant to non-migrant ratio suggested by Baker (1978).

The total populations of the two quarters to be compared are unlikely to be identical in size and must be normalised such that the difference indicates a change in the distribution of the species rather than just a difference in its ease of detection. The Movement Participation Rate was calculated in two steps: (1) the 200-km grid-square reporting rates were normalised in both of the periods of interest by dividing each 200-km grid-square reporting rate by the sum of all such rates for the period, and (2) the absolute differences between the two time periods of corresponding 200-km normalised grid-square reporting rates were summed. As this sums both the positive and (the equal in magnitude) negative differences, the total was divided by two. A Movement Participation Rate of 50% would indicate that, between quarters, at least half of the total population appear to move between grid squares.

Population sums and ratios

Migrations of species into and out of survey sites are inferred from variations in counts of individuals (Ford *et al.* 1985; MacNally 1995, 1996). An analogous calculation may be performed using the Eastcoast database to estimate seasonal variations in the relative sizes of the species' populations within the entire eastern half of Australia. The relative population sizes of species were calculated by summing each of the landfall-corrected 200-km grid-square reporting rates of the species for each three-month quarter. For each species, variations in quarterly sums may indicate movements into or out of the eastern half of Australia, movements to areas in eastern Australia not adequately surveyed, or changes in detectability. The quarterly population sums provide very little information across species as their nominal values are greatly influenced by the behaviour of each species and the survey methods employed to detect them (Shields and Recher 1984; MacNally 1997). However, the size of the population change, as indicted by the ratio of the smallest and largest sums, can be compared. For example, a ratio value of 1.1 would indicate that the population size remained almost constant between quarters, as would be expected to occur for a sedentary and conspicuous species. However, a population ratio of 7.2 suggests that most of the population was not detected in the quarter with the lesser population sum, as would occur if the species were an intercontinental migrant.

Centroid vectors

It may be possible to detect a large migratory movement by a species by investigating the change in the geographical centre of the species' range, referred to as the 'centroid' (Fig. 3).

The data for this calculation consisted of the quarterly 200-km grid-squares for which there were reporting-rate estimates in both quarters being compared. The reporting rate of each grid-square was used as a weight for the contribution of that grid-square's coordinates to that quarter's centroid coordinates. The vector between the Australian Map Grid coordinates of the two centroids of the two quarters was determined using simple trigonometry and is referred to as the Centroid Vector. Variance estimates of the Centroid Vector's azimuth and magnitude were calculated via propagation of the variances of the differenced centroid positions (Lauf 1983). Note that the centroids in this context are mathematical constructs and are not intended to represent localities of any biological significance. As such, there is no issue with concave (U-shaped) or complex range distributions such as occurs when estimating the centroid of an individual bird's home range (Anderson 1982). Although Centroid Vectors are crude in that they will not detect an omni-directional expansion or retraction of the range, or combinations of movements whose effects cancel each other out, they do detect a general shift in the range.

Seasonal maps

A series of maps of ranges, preferably with some shading to reflect reporting rates, may provide an abundance of information that cannot be conveyed in a single map (Harrison 1991). It may be possible to identify over-wintering and possible breeding areas (when combined with breeding-activity data), regions containing sedentary populations, areas of greatest density flux, areas transited but not occupied for a substantial fraction of the year, and the general directions and patterns of movement.

The fundamental unit of measurement of the atlas data is the reporting rate, which is derived from many surveys at non-gridded locations surveyed at different times. Further complicating the mapping process are the patchy distributions of many species. Because of these attributes, a similar approach was used to that of Butler *et al.* (1995), who derived continuous reporting rate values along transects from discrete bird counts by a technique referred to as 'boxcar smoothing'. 'Boxcar smoothing' can be extended to two or more dimensions, as described by Cressie (1991), to calculate what Cressie labelled a 'space–time autoregressive moving average'. An advantage of this method, besides its simplicity, is that it will not result in nonsensical negative reporting-rate estimates, as may occur using some modelling techniques. Maps were produced with a 20-km map-point resolution (pixel size) using surveys carried out predominately within the 91-day quarter and within 150 km of the map-point. Details of the map-point distance and time weight functions are given in Griffioen (2001).

Species movement classification

Each of the atlas-data-derived indicators used to describe changes in species' distributions cannot be solely relied upon to detect bird movements. Thus, combinations of indicators were used to separate

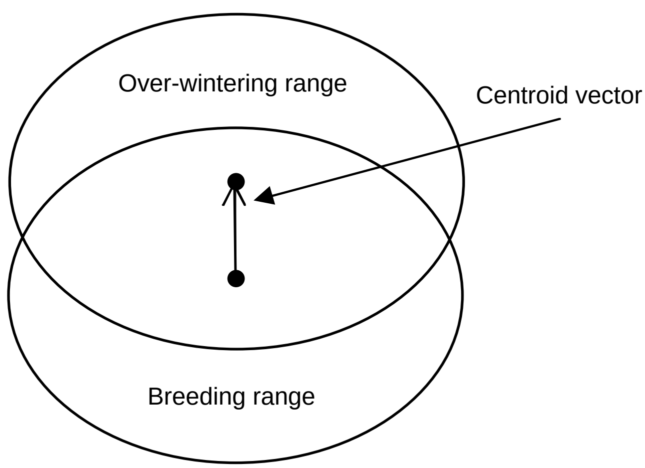


Fig. 3. A simplified diagram of the Centroid Vector. The Centroid Vector is the vector between the two centroids of the ranges of a species mapped at different times. It provides an estimate of the average minimum distance and direction of the shift in the range.

species into three groups: large-scale movements present, sedentary or insufficient evidence (Table 2). Due to limitations of the data, analyses were based upon a 200 km by 200 km grid overlaid on eastern Australia. Hence only 'large-scale movements', as opposed to those less than 200 km, could be detected. The three primary indicators used to separate species into these groups were the Spatial Distribution Test, the Centroid Vectors and the range map sequences. The Population Ratio and the Movement Participation Rate were used as secondary evidence. Note that the 'large-scale movements present' group of species includes full migrants, partial migrants and nomads, as defined by Rowley (1975).

For each species classification it was essential that evidence of the large-scale movement or sedentary behaviour was visually apparent on the range map sequences. Thus, species for which there were too few observations to create representative range maps were automatically classified as 'insufficient data' regardless of the results of the other indicators.

Within the large-scale movements and sedentary groups, species were further subdivided into those with 'strong evidence' and those with only 'suggestive evidence'. Strong evidence of movements consisted of a significant Spatial Distribution Test result and/or Centroid Vector, in conjunction with very obvious changes in the species' range within the maps. In addition, if both the Population Ratio and the Movement Participation Rates were high and were accompanied by obvious changes of range distribution of the species throughout the year, then these species were also classified as having 'strong evidence' of movements. This additional test was included so that intercontinental migrants, which may not be detected by the Spatial Distribution Test, would be classified correctly.

Species were classified as having 'suggestive evidence' of movements if obvious changes in the species distribution were present in well surveyed areas of the range maps (generally the south-eastern coast of Australia), but were not evident in the mathematical indicators.

Species were classified as having 'strong evidence' of being sedentary if their Spatial Distribution Test result was not significant ($1 - P < 0.95$), they had low Population Ratios (<2.0) or Movement Participation Rates (<20%), and the range maps indicated that their range and distribution remained constant. Species were classified as having 'suggestive evidence' of being sedentary if their range maps indicated that their range and distribution remained constant, regardless of the values of the mathematical indicators.

Movement pattern classification

The range maps of species for which large-scale movements were detected were carefully examined for evidence of patterns of movement. With the aid of the Centroid Vector diagrams, simplified depictions of movement patterns were created for each species. Species with broadly similar movement patterns were then grouped. Similarities and differences between groups were noted and generalised maps formed. While the generalisation process was subjective, the aim of this procedure was to produce regional movement pattern archetypes in the hope that these might stimulate future consideration of the ecological factors leading to these common patterns. All of the indicators and range maps used for the 407 species' movement and pattern classifications used in this study have been compiled on compact disk, together with viewing software, by the senior author, and are available from him on request.

Results

Species examples

Four species were chosen as case studies as they were representative of a variety of suspected movement patterns, from migratory to sedentary and because they highlight different a pects of the assessment process.

Dollarbird

The Dollarbird has long been regarded a migratory species that overwinters outside Australia (Higgins 1999). The spatial distribution of the Dollarbird varied significantly ($P = 0.0014$) (Fig. 4*A*) between the 'breeding' and 'over- wintering' quarters. Of the four quarterly difference spatial distribution statistics, the 'post-breeding' to 'over-wintering' and the 'pre-breeding' to 'breeding' quarters statistics failed to reach significance ($P = 0.9106$ and $P = 0.6339$ respectively) (Fig. 4*A*). However, the spatial distribution test of Syrjala (1996) utilises normalised densities and thus is insensitive to the immense population size increase and decrease as indicated by the population ratio of 58.3 (Fig. 4*B*). For these two quarterly

Table 2. The method used for classifying species either as undertaking large-scale movements, being sedentary or having 'insufficient data' to determine their large-scale movement status

In addition, both the large-scale-movement groups and sedentary groups were further subdivided as to whether there was 'strong' or 'suggestive' evidence for their classification in the five movement indicators. This resulted in ten Movement Evidence Groups being defined

	Movement Evidence Group	Spatial Distribution Test ($1 - P > 0.95$)	Centroid Vector significance > 0 ($P < 0.05$)	Range maps	Population ratio	Movement Participation Rate
Large-scale movements Strong evidence	1	Significant	Significant	Obvious changes	Not considered	Not considered
	2	Significant	Not significant	Obvious changes	Not considered	Not considered
	3	Not significant	Significant	Obvious changes	Not considered	Not considered
	4	Not significant	Not significant	Obvious changes	>3.0	>40%
Large-scale movements Suggestive evidence	5	Not significant	Not significant	Obvious changes in well surveyed areas	Not considered	Not considered
Sedentary Strong evidence	6	Not significant	Not significant	No significant change in range	<2.0	Not considered
	7	Not significant	Not significant	No significant change in range	Not considered	<20%
Sedentary Suggestive evidence	8	Significant	Not significant	No significant change in range	Not considered	Not considered
	9	Not significant	Not significant	No significant change in range	>2.0	>20%
Insufficient data	10			Range not adequately mapped		

differences, the pattern of distribution of the species across its range and the range itself were not detected as significantly changing. This is far more obvious in the comparison of the 'pre-breeding' and 'breeding' range maps than the 'post-breeding' and 'over-wintering' maps (Fig. 5).

The Centroid Vector diagram indicates a significant north-north-west movement of 822 km ($P < 0.05$, s.d. = 189 km) (Fig. 4*C*) in the range centroids between the 'breeding' and 'over-wintering' quarters. It should be noted that as most of the population appear to over-winter abroad, the Centroid Vector magnitude is not representative of the average distance travelled by this species, but merely indicates the significant shift between the 'breeding' and 'over-wintering' ranges of this species within Australia. This statistic, coupled with the Movement Participation Rate of 80% (Fig. 4*A*), indicates that the migratory pattern of the Dollarbird is very strong and almost complete. The between-quarters Centroid Vectors indicate that the northward 'over-wintering' journey is somewhat evenly split over two quarters whereas the southward invasion occurs almost entirely in 'over-wintering' to

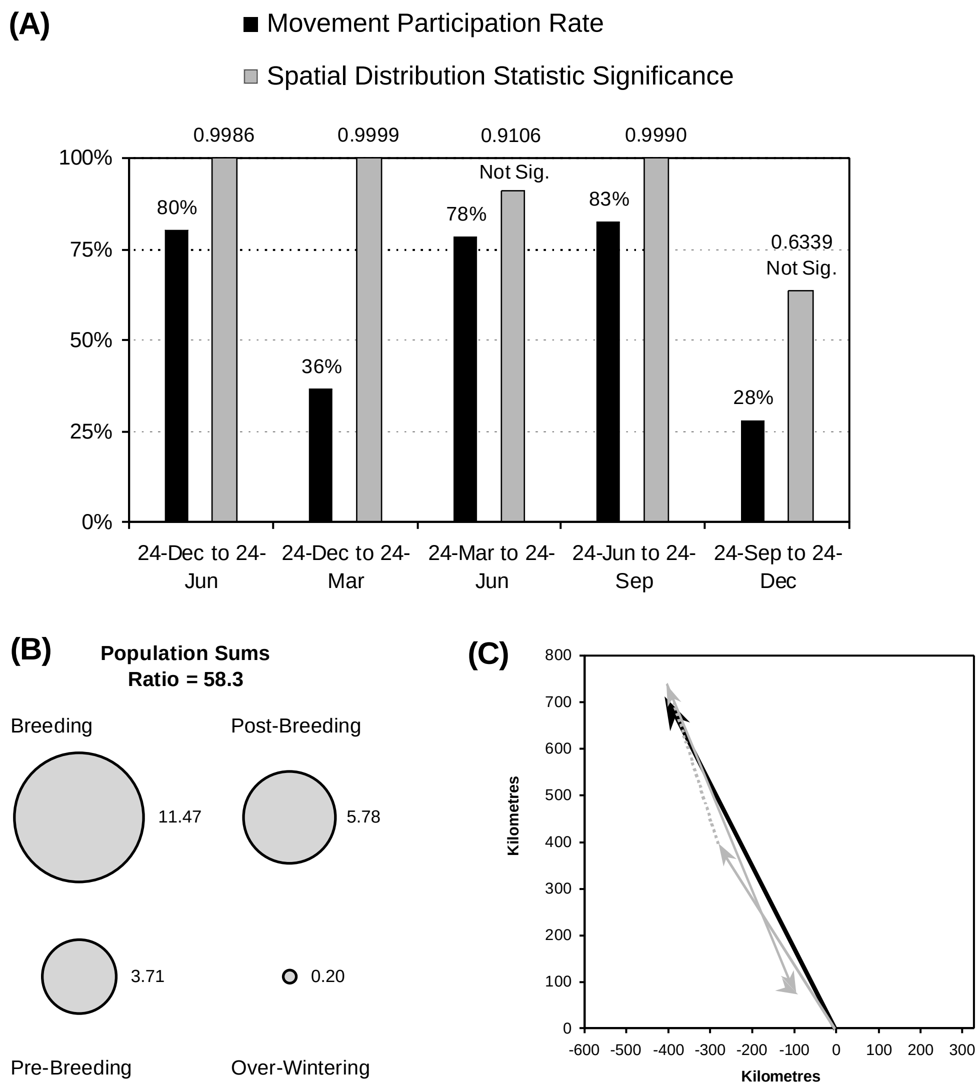


Fig. 4. Graphical representation of the quarterly statistics for the Dollarbird. The mid-point of the Dollarbird's breeding season was 24 December (n = 37 nests, s.d. = 15 days). (*A*) The 'breeding' versus 'over-wintering' Spatial Distribution Statistic (solid bar) and Movement Participation estimate (striped bar) are presented along with their respective between-quarter values. Non-significant ($1 - P < 95\%$) Spatial Distribution Statistic values are indicated. (*B*) The relative size of the quarterly population sums. (*C*) The diagram of the between-quarters Centroid Vectors. The thick Centroid Vector has been calculated between 'breeding' and 'over-wintering' quarters and it is significantly ($P < 0.05$) greater than zero. The four between-quarters Centroid Vectors are given by the four sequential thin grey arrows. Two of the four between-quarters Centroid Vectors (thin solid lines) are significantly greater than zero ($P < 0.05$), whereas the hatched vectors are not.

'pre-breeding' quarters. This does not indicate that birds arrive only between the 'over-wintering' and 'pre-breeding' quarters, as the population sums clearly indicate that this is not the case. What it does indicate, however, is that birds arriving closer to the 'breeding' quarter distribute themselves evenly over the range, which covers its fullest extent by the 'pre-breeding' quarter. This is quite unlike the northward journey, in which the range retreats over two quarters.

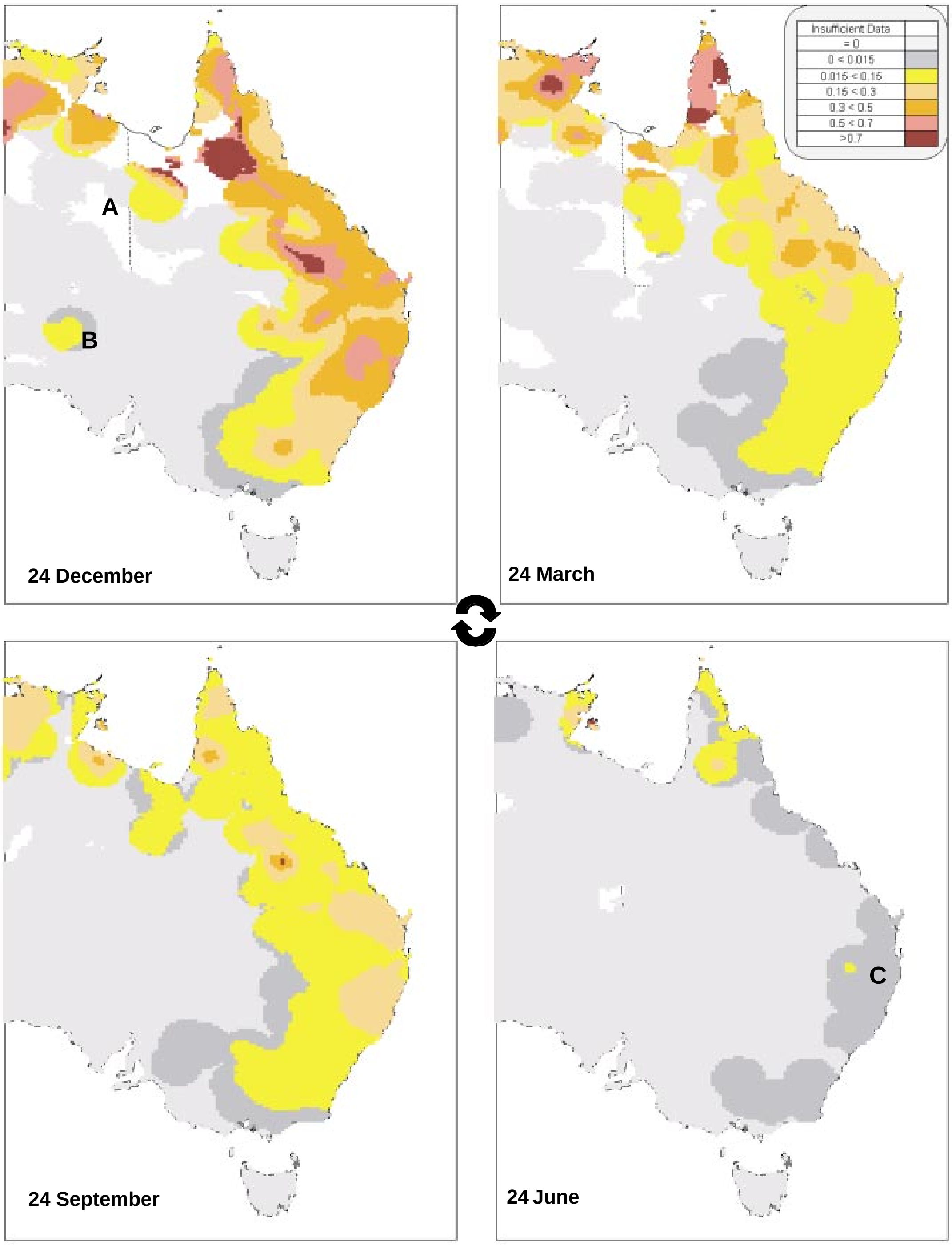


Fig. 5. Average reporting rate maps for the Dollarbird. These maps are centred on the 'breeding' (top left), 'post-breeding' (top right), 'over-wintering' (lower right) and 'pre-breeding' (lower left) quarters. The paucity of survey data in remote regions (marker A) does not support mapping of reporting rate values in this area. The Dollarbird observation at marker B may either be a vagrant or an error of position. The records of Dollarbirds in the 'over-wintering' map (marker C) result from the inclusion of long surveys (>91 days), for which the centre date of each survey falls within the quarter.

The range distribution maps (Fig. 5) suffer from the lack of data in the north during the 'wet' season, as is the case in all of the range maps in this study (marker *A*). Likely errors of survey position or species identification are evident in the 'breeding' range map (marker *B*), Unfortunately there is no evidence available to support or refute this supposition. Given the highly migratory nature of the species, it is possible that a vagrant has been sighted in western South Australia. Finally, it should be noted that the low-density dark grey areas in the 'over-wintering' range map (marker *C*) make it appear that some birds are present in the south throughout the winter. Although the Dollarbird appears to remain in northern areas throughout the year and has been recorded migrating north from southern areas as late as May (Higgins 1999), those marked as remaining in the south may result from a combination of the survey and legend selection process rather that actual sightings in the middle of winter. For each quarter, any survey with a mid-survey date falling within the quarter (in this case 24 June ± 45 days) and for which most of the survey occurred in that quarter, are included in the quarter. Thus, observations from long surveys (up to 91 days) for which the mid-survey date falls near the edge of the quarter are included on this map. The 'over-wintering' quarter map centred on 24 June includes Dollarbirds sighted from 27 March until 11 September, which encompasses their early arrival and late departure dates (Higgins 1999). Even though these observations attract very low weights in the averaging scheme, the resultant regional reporting rate is non-zero and thus these points plot in this legend range.

Noisy Miner

Detailed studies of the Noisy Miner, based on long-term monitoring of colour-banded individuals, suggest that this species is sedentary (Dow 1978). The spatial distribution test did not detect significant variation in the Noisy Miner's range between the 'breeding' and 'over-wintering' quarters ($P = 0.1942$). The population ratio of 1.2 for this species indicates that the population appears stable and the Noisy Miner's range is well surveyed throughout the year (Fig. 6). Only 11% of the population was estimated as moving between these times. As this species is known to be sedentary (Dow 1978), this value quantifies the noise on the participation rate estimate. There was only an 11-km shift in the range centroids between periods, which was non-significant ($P > 0.05$, s.d. = 64 km). The range maps depict 'breeding' and 'over-wintering' ranges that do not vary substantially in shape (Fig. 7). The 'over-wintering' map displays slightly higher species densities, which is supported by the population sum graph. In short, all of the evidence presented indicates that this species is sedentary.

Grey Fantail

The Grey Fantail has six subspecies in Australia with isolated breeding ranges (Blakers *et al.* 1984). Two of these are suspected to be sedentary, one nomadic and three migratory (Blakers *et al.* 1984). As subspecies are not differentiated in the Eastcoast database, the results presented are a conglomeration of the behaviours of at least four of these subspecies.

The spatial distribution statistics (Fig. 8) indicate that the Grey Fantail exhibits significant variation in range distribution between the 'breeding' and 'over-wintering' quarters ($P = 0.0001$). Each quarter-to-quarter range distribution was significantly different ($P \leq 0.0260$). It is interesting to note that the Movement Participation statistic between the 'breeding' and 'over-wintering' quarters (51%: Fig. 8) nearly equates to the sums-of-pairs component quarter-to-quarter moving statistics (25% + 35% and 22% + 42%). This suggests that movements of this species form a continuous flow throughout the year, unlike the Dollarbird. This is supported by the range maps (Fig. 9), which depict a tide of birds moving up and down the east coast of Australia. The four

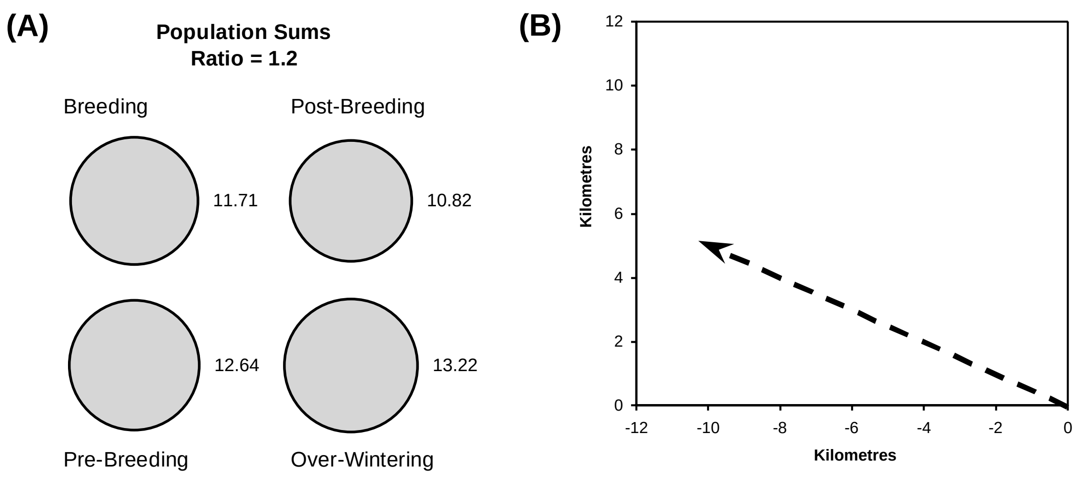


Fig. 6. (*A*) Graph indicating the relative sizes of the quarterly population sums for the Noisy Miner. (*B*) Graph depicting the non-significant 'breeding' *versus* 'over-wintering' Centroid Vector of 11 km ($P > 0.05$, s.d. = 64 km).

quarter-to-quarter Centroid Vectors sum very nearly to the significant 'breeding' to 'over-wintering' vector of 640 km ($P < 0.05$, s.d. = 105 km), suggesting good coverage of the range of this species throughout the year. Only two of the four quarter-to-quarter vectors were significantly larger than zero (solid arrows as opposed to dashed arrows in Fig. 8*C*) and these corresponded to the quarter transitions experiencing the largest Movement Participation rates ('post-breeding' to 'over-wintering' and 'pre-breeding' to 'breeding). The Centroid Vector diagram (Fig. 8*C*) indicates that the migratory movements of this species between the 'breeding' and 'over-wintering' quarters are likely to be large, coherent and aligned almost directly north. The vectors closely align along a single direction rather than creating a circular or crossed pattern. This suggests that this species retraces its path on the return migratory journey rather than taking, for example, a more inland route.

The population sum ratio of 2.1 warrants discussion. The quarterly population sums are lower when most of the population occupies the well surveyed southern portion of its range and rises as the density increases in the northern part of its range. There are a few possible explanations for this disparity. Perhaps there is decrease in conspicuous behaviour of the species during the breeding season with a corresponding increase in this behaviour, such as calling and displays, in the pre-breeding season. This may affect their likelihood of detection. This effect could be tested by examining the results of Grey Fantail reporting rates derived from exhaustive area searches and casual atlas-type searches of the same areas in different seasons. Alternatively, the 200-km grid-square reporting rates summed to form this value may overestimate the relative population size when the species range is more northward. During this period, the fantail occupies a higher proportion of areas that are poorly surveyed. If the surveys in these areas are biased towards suitable Grey Fantail habitat, such as woodland surrounded by plains, then the population may be overestimated. This bias could be detected by comparison of reporting rates of the whole 200-km grid-square to those partitions of the grid-square for which habitat information are available.

Fig. 9 provides the most succinct description of the Grey Fantail's migratory pattern. The varying form and timing of the Grey Fantail's range very closely maps the mean growth index charts presented by Nix (1976). The Grey Fantail appears to be an ideal species in which to investigate the influence of external stimuli such as photoperiod, temperature change and rainfall, on the timing and patterns of movements of birds.

Budgerigar

Rowley (1975) described the Budgerigar's movements as lacking a clear migratory pattern, labelling them nomadic, whereas Wyndham (1982) concluded that it had an underlying seasonal pattern of movements, which was highly influenced by rainfall. In eastern Australia, the Budgerigar predominantly breeds in the spring and summer in the south,

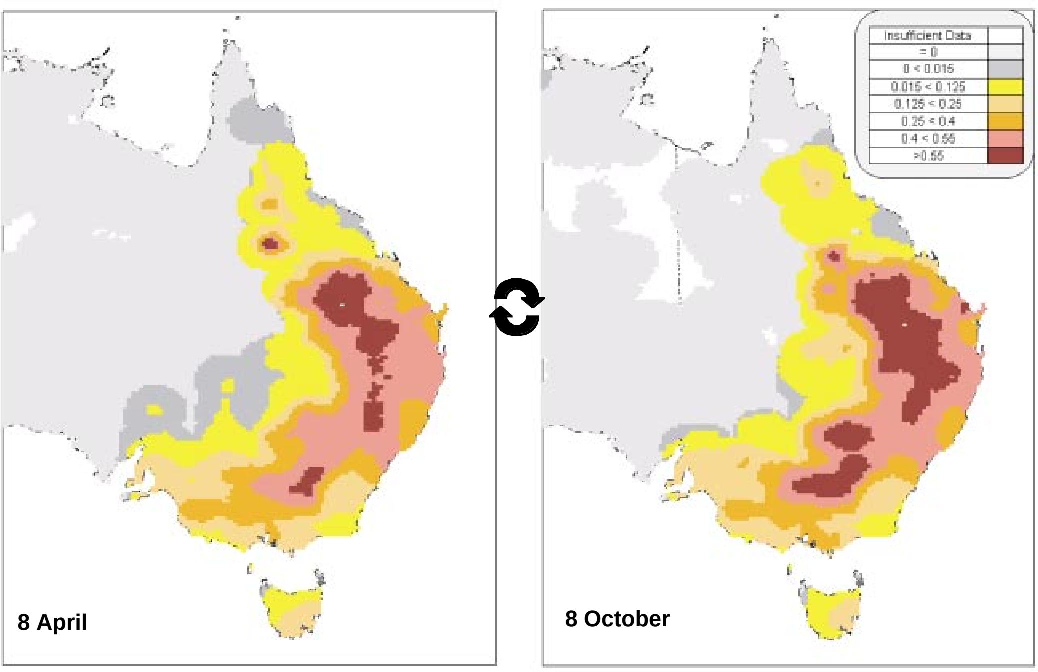


Fig. 7. Average reporting-rate maps for the Noisy Miner. These maps are centred on the 'breeding' (left), and 'over-wintering' (right) quarters. The mid-point of the Noisy Miner's breeding season was 8 October ($n = 608$ nests, s.d. = 53 days).

and in the winter and autumn in the north (Wyndham 1982). This accounts for the large standard deviation for the average breeding date (Fig. 10).

The spatial distribution statistic between the 'breeding' and 'over-wintering' quarters indicated a significant variation in the Budgerigar's range for these periods (P = 0.0001) (Fig. 10). The quarter-by-quarter analysis also detected significant range distribution variations in three out of four sequential quarter differences. The non-significance of the 'post-breeding' to 'over-wintering' quarters is evident in the range maps of these periods (Fig. 11). These two maps are the most similar of the four once the area of missing data in the 'post-breeding' map is discounted (marker A, Fig. 11). The lack of survey coverage is further highlighted by the low 'breeding' and 'post-breeding' population sums, which correlate with their corresponding range maps. Poor survey coverage of outback Queensland and the Northern Territory is common to all maps across the 'wet' season (November to March).

The Budgerigar appears to be fairly mobile throughout the year, with 30–45% of the population apparently moving between 200-km grid-squares. The Centroid Vector diagram indicates a significant north-north-west shift of 355 km from

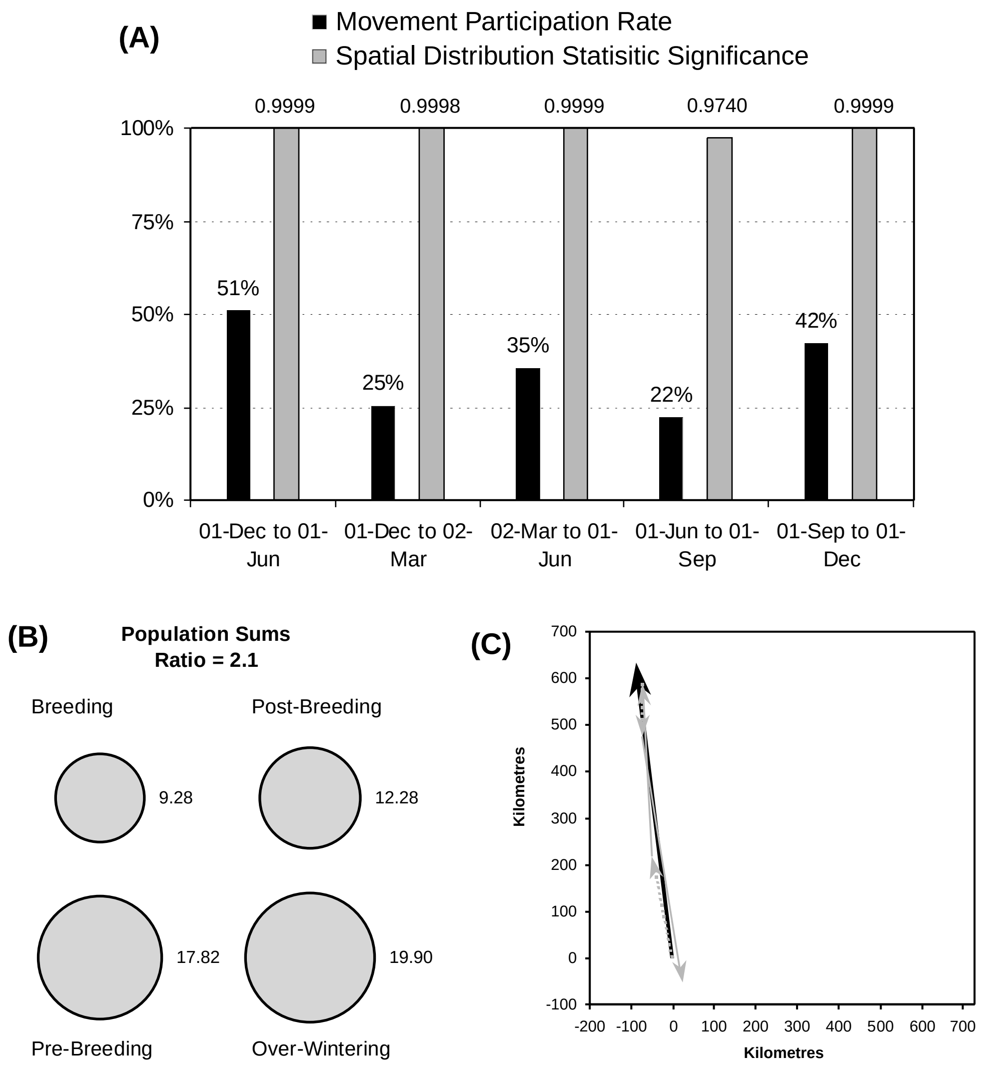


Fig. 8. Graphical representation of the quarterly statistics for the Grey Fantail. The mid-point of the Grey Fantail's breeding season was 1 December (n = 1065, s.d. = 32 days). (A) The 'breeding' *versus* 'over-wintering' Spatial Distribution Statistic (solid bar) and Movement Participation estimate (striped bar) are presented along with their respective between-quarter values. All of the Spatial Distribution Statistic values were significant ($P < 0.05$). (B) Graph of the relative size of the quarterly population sums. (C) Graph depicting the size and direction of the Centroid Vectors. The thick black Centroid Vector has been calculated between 'breeding' and 'over-wintering' quarters and it is significantly ($P < 0.05$) greater than zero. The four between-quarters Centroid Vectors are given by the four sequential grey arrows. Two of the four between-quarters Centroid Vectors (thin solid lines) are significantly greater than zero ($P < 0.05$).

the ‘breeding’ centroid to the ‘over-wintering’ centroid ($P \leq 0.05$, s.d. = 82 km). This shift is clearly evident in the range maps, with the Budgerigar retreating from Victoria, the south-western plains of New South Wales and south-eastern South Australia (marker B, Fig. 11). During this time, the Budgerigar retreats further inland away from the south-eastern Queensland coast (marker C, Fig. 11) and the South Australian coast (marker D, Fig. 11). Increases are concurrently occurring in outback regions such as Longreach, Birdsville and the Barkly Tablelands (markers E, F and G respectively, Fig. 11). The summation of all of these shifts would account for the significant Centroid Vector. The

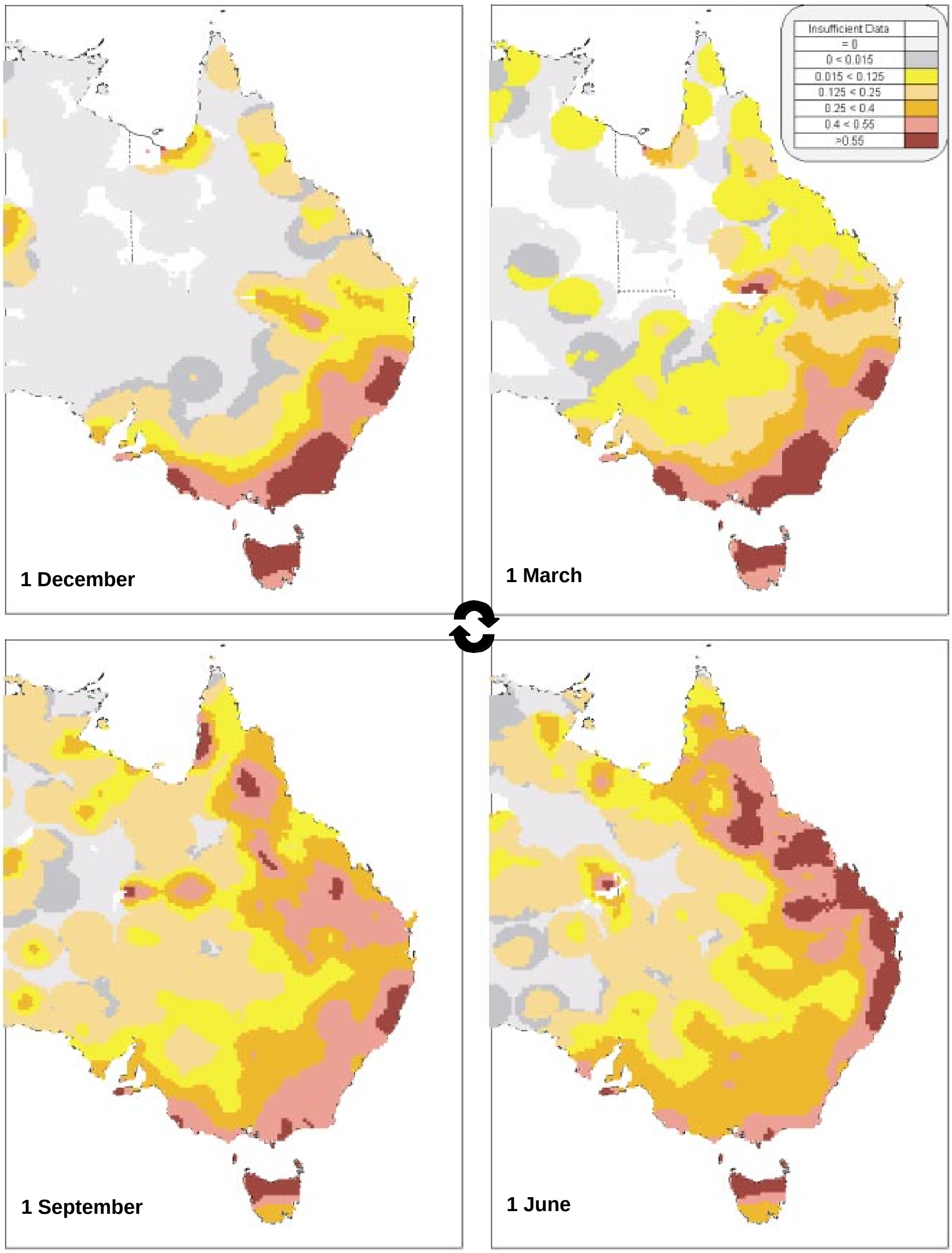


Fig. 9. Average reporting-rate maps for the Grey Fantail. These maps are centred on the ‘breeding’ (top left), ‘post-breeding’ (top right), ‘over-wintering’ (lower right) and ‘pre-breeding’ (lower left) quarters.

increase in reporting rates of the Budgerigars in the Nullarbor Plain during the 'pre-breeding' season (marker H, Fig. 11) would be interesting to verify as there is little evidence of high densities in this region at other times of the year.

Further analysis of movement patterns of this species will require much more survey data from remote regions. This general pattern of movement is consistent with the movements postulated by Wyndham (1982) and other anecdotal records summarised in Higgins (1999). The approach used in our analysis cannot detect the many and varied non-regular movements cited in Higgins (1999) due to the compression of all surveys into one theoretical year. However, given sufficient data, these methods should be able to eventually detect those movement components that are repeated, albeit infrequently.

Species movement classification

A total of 145 species (36.9% of 393 species) for which there were sufficient data for analysis were detected as undertaking large-scale movements (Table 3). The remaining 248 species (63.1%) appeared to be sedentary. There were

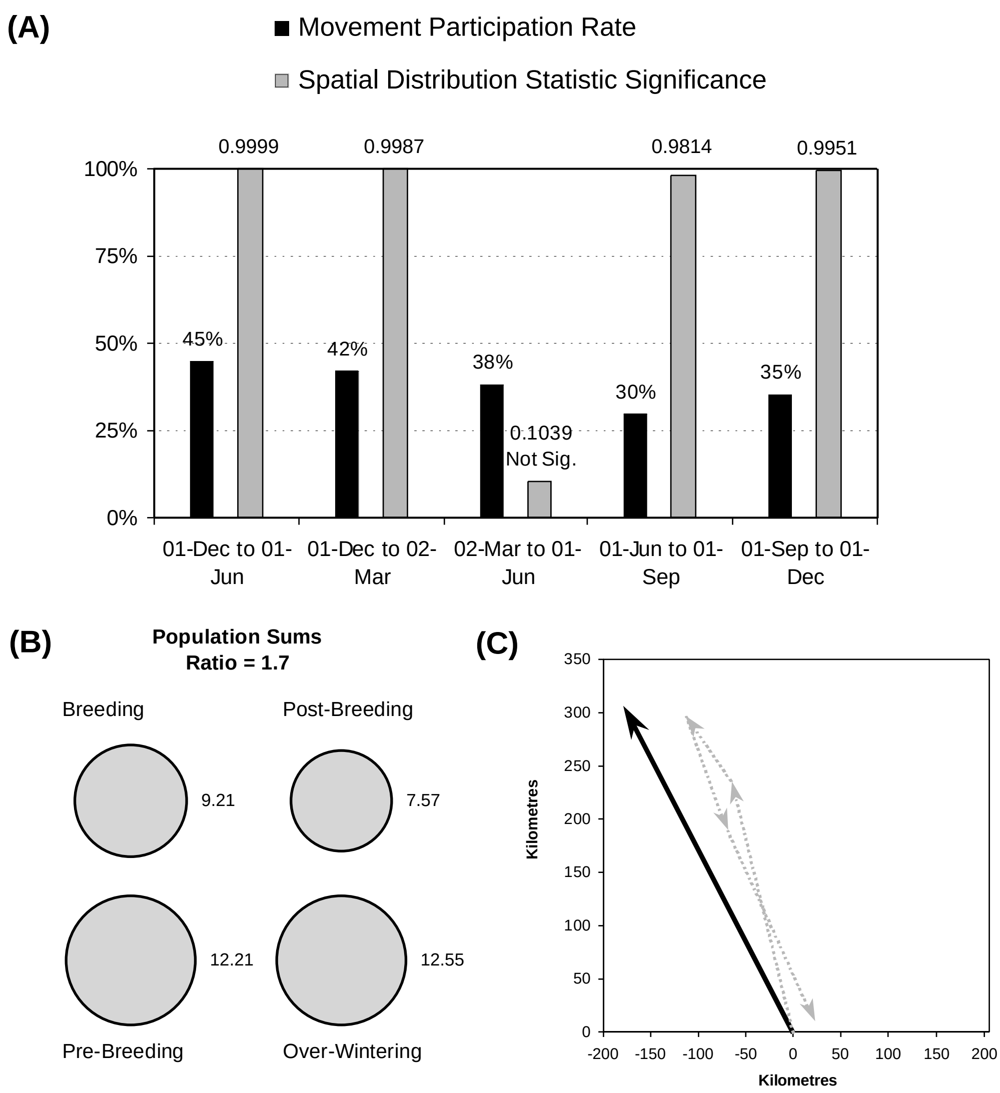


Fig. 10. Graphical representation of the quarterly statistics for the Budgerigar. The mid-point of the Budgerigar's breeding season is the 1 December (n = 130, s.d. = 83 days). (*A*) The 'Breeding' *versus* 'over-wintering' Spatial Distribution Statistic (solid bar) and Movement Participation estimate (striped bar) are presented along with their respective between-quarter values. (*B*) The relative size of the quarterly population sums. (*C*) The diagram of the between-quarters Centroid Vectors. The thick black Centroid Vector was calculated between 'breeding' and 'over-wintering' quarters and it was significantly ($P < 0.05$) greater than zero. The four between-quarters Centroid Vectors are given by the four sequential thin grey hatched lines, all of which were not significantly ($P > 0.05$) greater than zero.

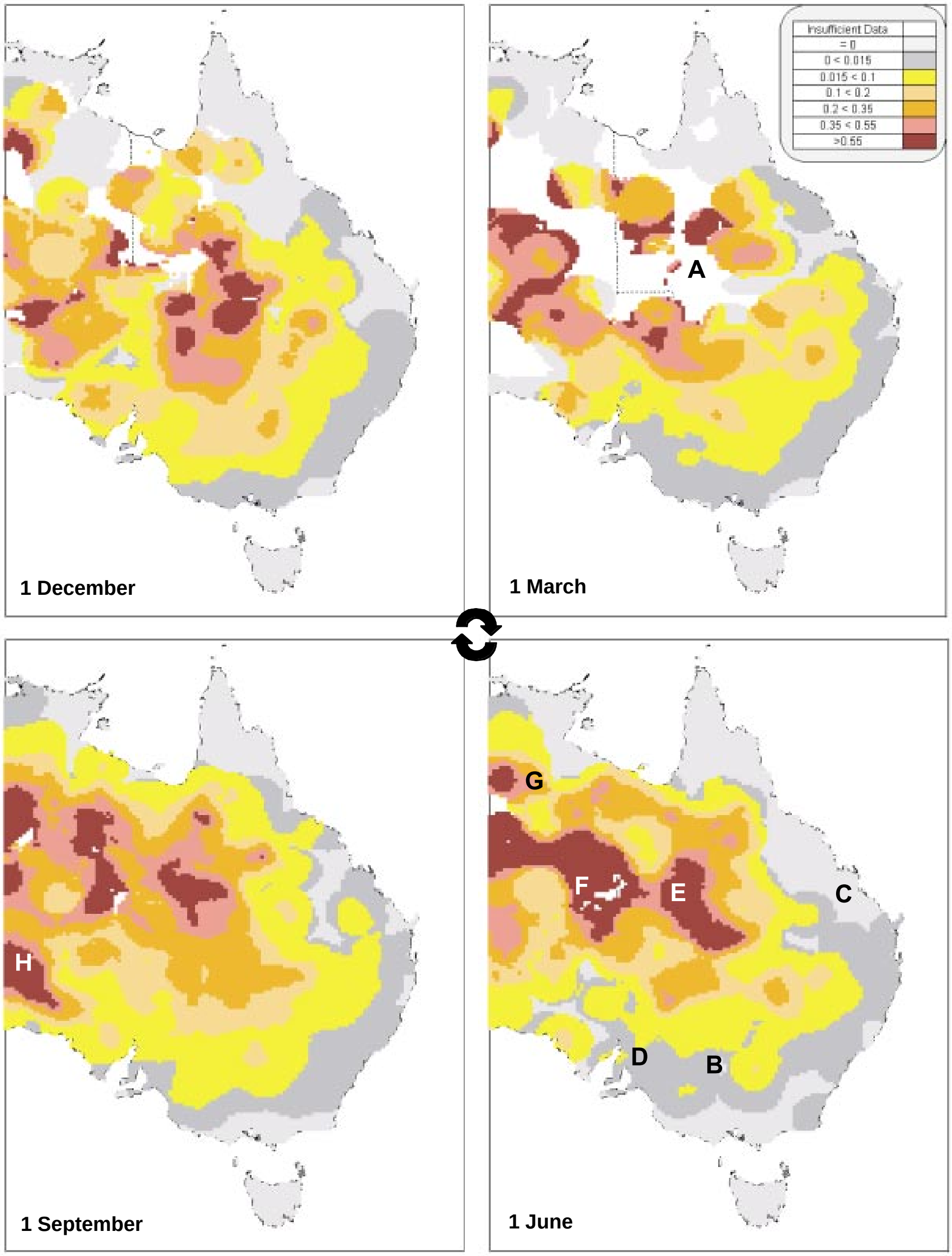


Fig. 11. Average reporting-rate maps for the Budgerigar. The maps are centred on the 'breeding' (top left), 'post-breeding' (top right), 'over-wintering' (lower right) and 'pre-breeding' (lower left) quarters. During the 'post-breeding' quarter, there are insufficient data in the rural areas of Queensland (marker A) to support mapping of the reporting rates. The Budgerigar appears to move away from coastally influenced regions (markers B, C and D) during the 'over-wintering' quarter. Increases are concurrently occurring in outback regions such as Longreach, Birdsville and the Barkly Tablelands (markers E, F and G respectively). There is an interesting increase in reporting rates of the Budgerigars in the Nullarbor Plain during the 'pre-breeding' season (marker H).

insufficient data to assess the movement classification of 14 species. The results for all 407 species are listed in the Appendix*. Each one of the three classification groups are described below.

*Available from the author, from the journal on request (PO Box 1139, Collingwood, Vic. 3066, Australia), or from the internet at http://www.publish.csiro.au/journals/ap/mu/102/1/MU01024_AC.pdf

Table 3. The number of species detected as undertaking large-scale movements, those that are sedentary, and those for which there were insufficient data to determine their movement classification

The number of birds with both 'strong' and 'suggestive' evidence for each classification and their corresponding Movement Evidence Groups (see Table 2) are also listed

	Movement Evidence Group	No. of species
	1	44
Movements present	2	49
Strong evidence	3	2
	4	6
Movements present Suggestive evidence	5	44
Sedentary	6	185
Strong evidence	7	10
Sedentary	8	26
Suggestive evidence	9	27
Insufficient data	10	14
Total		407

Species undertaking large-scale movements

There was strong evidence of large-scale movements for 101 species (Table 3, see Appendix for details). Two species (the Barn Owl, *Tyto alba*, and the Little Grassbird, *Megalurus gramineus*) were classified as undertaking large-scale movements on the basis of significantly large Centroid Vectors and the changes evident in their ranges. In addition, these species had Movement Participation Rates greater than 50%, and yet both of these species had non-significant Spatial Distribution Test results.

A further six species were classified on the basis of their high Population Ratios and Movement Participation Rates along with obvious changes in their range map sequences. Of these six species, two were intercontinental migrants (Pied Imperial-Pigeon, *Ducula bicolor*, and Metallic Starling, *Aplonis metallica*) while the other four have large and sparsely populated ranges (Square-tailed Kite, *Lophoictinia isura*, Whiskered Tern, *Chlidonias hybridus*, Red-browed Pardalote, *Pardalotus rubricatus*, Black-chinned Honey-eater, *Melithreptus gularis*).

Sedentary

In total, 248 species were detected as sedentary (Table 3, see Appendix for details). The range maps for some of these species did vary between periods, but the variations in the sizes of the ranges, or the distribution of birds within them, were judged to be the result of noise in the measurements rather than being due to long-distance movements by the species concerned. However, the resolution of this study must be taken into account. Species undertaking obvious highly localised movements may not be detected by these methods given the 200-km grid-squares used for most of the calculations. The Swift Parrot, *Lathamus discolor*, is one such example, being a known trans–Bass Strait migrant (Higgins 1999) and yet it was not detected by these methods at the resolution used to examine the data.

Insufficient data

For 14 species the data were insufficient to classify their movements (see Appendix for details). All of these species were poorly represented in the Eastcoast database. This is due to some of these species being cryptic (such as Baillon's Crake, *Porzana pusilla*, and the Australian Spotted Crake, *Porzana fluminea*), while others, such as the White-throated Nightjar, *Eurostopodus mystacalis*, occupy large ranges over which they were seldom seen. As a result, there were fewer than 1000 observations in the entire database for most of these species, and these observations were then subdivided into quarters for mapping and analysis. This paucity of data created discontinuous and sketchy distribution maps from which patterns were difficult to discern.

Species pattern classification results

Generalisation and classification of the 145 species detected as undertaking large-scale movements resulted in 18 movement patterns being identified. However, a number of species could well be classified in either of two or more of the patterns presented. As more data become available, it is likely that such borderline species will either more convincingly occupy a currently defined pattern, or further patterns will be defined to more accurately describe the observed variations in species' reporting rates.

Long-distance movement patterns

The long-distance movement patterns observed in the atlas data may be divided into two loosely defined groups: patterns aligned with the east coast, and inland patterns. One must bear in mind that for some species there exists some overlap between these groupings. Each group of patterns and the species assigned to them are described below. A generalised map is given for each pattern. Note that for each map, the arrows show the direction of movement from the areas occupied during the 'breeding' quarters to the areas occupied during the 'over-wintering' quarters. The arrows are not intended to imply that the total population in the regions are involved in the movement pattern. Nor are they intended to describe the pattern of movement over the entire range of the species. The arrows simply indicate the approximate directions, sources and destinations of the major pattern of movements apparent in the atlas data. Where a pattern has been generalised to include a number of similar patterns exhibited by assorted species, it may include dashed arrows, which signify that only some of the species in the group are likely to follow this route. For example, the Grey Fantail, *Rhipidura* *fuliginosa*, and the Rufous Fantail, *Rhipidura fuliginosa*, are both grouped in the 'Whole East Coast' pattern, but only the Grey Fantail migrates to Tasmania to breed. This is indicated by a dashed arrow between Tasmania and the mainland. The species to which these dashed arrows apply are obvious when the ranges of each species in the group are considered.

Coastal movements

These patterns are generally aligned or defined by the coast of eastern Australia. Most of the species within this grouping do not occupy inland regions of Australia although there are some exceptions. The species that do occupy both inland and coastal regions are included in this grouping because most of their population or movements appear to occur in the coastal regions. Note that the transition point between inland and coastal regions is somewhat arbitrary as is dictated by the high smoothing radius (150 km) employed in the range map production.

The coastal group can be further subdivided into trans–Bass Strait, eastern coastal, inter-continental coastal and reverse coastal migrants.

Trans–Bass Strait migrants

The five trans–Bass Strait migrants are given in Fig. 12. Although other species such as the Silvereye, *Zosterops lateralis*, and Grey Fantail also cross Bass Strait, the major movement undertaken by these five species is a northerly migration from Tasmania to close-by mainland areas during the winter months. The Fairy Tern, *Sterna nereis*, appears to migrate between coastal Tasmania and South Australia. It is not clear from the atlas data whether movements of this species along the Victorian coast are occurring. The Flame Robin appears to migrate both out of Tasmania and the highland areas of Victoria and southern New South Wales during the over-wintering quarter to further regions inland and western Victoria. This is best described as a fan out of Tasmania and Victoria.

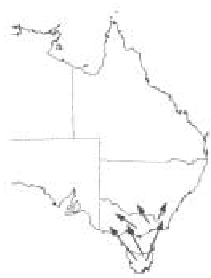
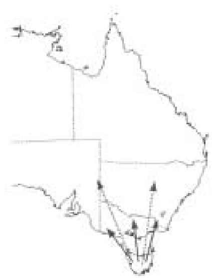
Pattern	Species	Map of Movement
Tasmania to South Australia 1 species	**Fairy Tern (*Sterna nereis*)**	
Tasmania & Victoria Fan 1 species	Flame Robin (*Petroica phoenicea*)	
Tasmanian Fan 3 species	**Blue-winged Parrot (*Neophema chrysostoma*)** **Pink Robin (*Petroica rodinogaster*)** Olive Whistler (*Pachycephala olivacea*)	

Fig. 12. The 'Trans–Bass Strait' patterns of movement. The major movement undertaken by these species is a northerly migration from Tasmania to close-by mainland areas during the 'over-wintering' quarter. Species whose names are shown in bold had strong evidence for their movement classification and those not in bold had only suggestive evidence.

Three species, the Blue-winged Parrot, *Neophema chrysostoma*, the Pink Robin, *Petroica rodinogaster*, and the Olive Whistler, *Pachycephala olivacea*, exhibit what was named the 'Tasmanian Fan' pattern. These species migrate out of Tasmania to varying extents inland on mainland Australia.

Eastern coastal patterns of movement

The eastern coastal migrant patterns (Fig. 13) are characterised by species that move along the eastern coast of Australia. Some of these species (such as the Scarlet Honeyeater, *Myzomela sanguinolenta*, and the Rose Robin, *Petroica rosea*) align closely with the coast whereas others (such as the Silvereye), move along the coast and through inland areas. The three species assigned to the 'South Y' pattern are characterised by the northward movement of birds from Tasmania during the winter months and movements through south-eastern Australia. The patterns of movement exhibited by the Yellow-faced Honeyeater and the Rose Robin are very

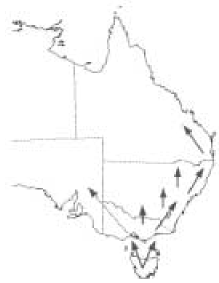
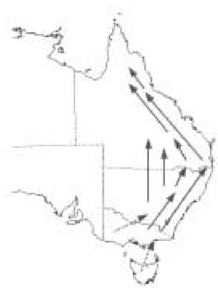
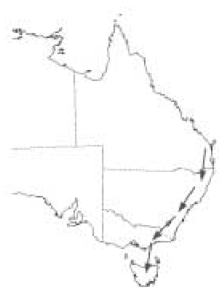
Pattern	Species	Map of Movement
South Y 3 species	**Golden Whistler (*Pachycephala pectoralis*)** **Dusky Woodswallow (*Artamus cyanopterus*)** Silvereye (*Zosterops lateralis*)	
Mid East Coast 4 species	**Yellow-faced Honeyeater (*Lichenostomus chrysops*)** **Scarlet Honeyeater (*Myzomela sanguinolenta*)** **Rose Robin (*Petroica rosea*)** Spectacled Monarch (*Monarcha trivirgatus*)	
Whole East Coast 6 species	**Fan-tailed Cuckoo (*Cacomantis flabelliformis*)** **Shining Bronze-Cuckoo (*Chrysococcyx lucidus*)** **Noisy Friarbird (*Philemon corniculatus*)** **Satin Flycatcher (*Myiagra cyanoleuca*)** **Rufous Fantail (*Rhipidura rufifrons*)** **Grey Fantail (*Rhipidura fuliginosa*)**	
Reverse South-East Coast 1 species	Cattle Egret (*Ardea ibis*)	

Fig. 13. The eastern coastal patterns of movement. This group of patterns is defined by species that move along the eastern coast of Australia. Species whose names are shown in bold had strong evidence for their movement classification and those not shown in bold had only suggestive evidence.

similar to the 'South Y' pattern except that these birds' ranges do not extend to Tasmania and therefore they were placed in the 'Mid East Coast' pattern grouping.

The 'Mid East Coast' pattern was defined as northward east-coast migrations (during the winter months) whose ranges and movements are more restricted than those in the 'Whole East Coast' pattern and for which most of the movement occurs very approximately in the mid regions of the east coast. This loosely defined group has a large variation in the mean latitude of the ranges of its four species.

The 'Whole East Coast' species are characterised by the size of their ranges, which encompasses most of the east coast of Australia, and the magnitude of their movements. All of the 'Whole East Coast' species are obvious migrants and were successfully detected by the Spatial Distribution Statistic as significantly changing their ranges between quarters.

The 'Reverse South-East Coast' pattern is unique in that this is the only pattern in which significant long-distance southern migration occurs during the winter months. This pattern is exhibited only by the Cattle Egret, *Ardeola ibis*, which has recently colonised Australia (Marchant and Higgins 1990).

Intercontinental coastal patterns of movement

The intercontinental group of species (Fig. 14) all exhibit high population ratios, indicating that it is likely that a large proportion of each population leaves eastern Australia during the winter months. The range map sequences of all of these species depict a rapid contraction of the range northward which reaches its maximum in the 'over-wintering' quarters. These patterns may involve migration along the coast, but it appears that most of the birds opt for the direct route north and, later, south. The ranges of some of the species listed in these patterns include the Northern Territory.

The 'International Whole Coast' pattern contains species that migrate as far south as New South Wales and, for some, Victoria. The 'International North Coast' pattern, however, contains only birds for which the southern extents of their ranges just reach into north coastal Queensland.

Inland patterns

The inland patterns of movement are difficult to categorise as this includes areas with relatively few surveys. Most of the range maps of the species in the inland regions are 'noisy' and often contain areas with insufficient data to calculate reporting rates for mapping. The patterns indicate in which part of the species' range change is occurring rather than describing the entire range of the species.

The inland patterns can be further sub-divided into two groups: predominantly north/south movements and non-cardinal-direction movements.

North/south inland patterns

Three north/south inland patterns of movement were evident (Fig. 15). The 'Mid Line North' pattern was assigned

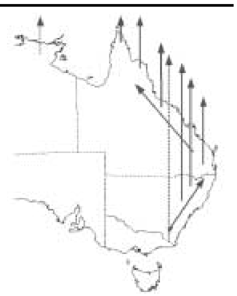
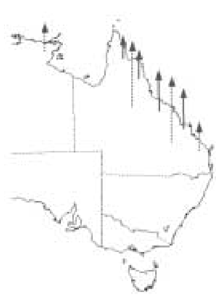
Pattern	Species	Map of Movement
Intercontinental, Whole Coast 7 species	Little Tern (*Sterna albifrons*) **Brush Cuckoo (*Cacomantis variolosus*)** **Common Koel (*Eudynamys scolopacea*)** **Channel-billed Cuckoo (*Scythrops novaehollandiae*)** **Dollarbird (*Eurystomus orientalis*)** **Black-faced Monarch (*Monarcha melanopsis*)** **Cicadabird (*Coracina tenuirostris*)**	
Intercontinental, North Coast 3 species	Superb Fruit-Dove (*Ptilinopus superbus*) **Pied Imperial-Pigeon (*Ducula bicolor*)** **Metallic Starling (*Aplonis metallica*)**	

Fig. 14. The coastal intercontinental patterns of movement. These birds breed in Australia during the summer months and then most migrate north out of the country. Species whose names are shown in bold had strong evidence for their movement classification and those not shown in bold had only suggestive evidence.

to species that migrated directly northward for the 'over-wintering' quarter but did not proceed onward to the northern Australian coast. The movements of these species did not appear to be influenced by the shape of the east coast other than it acting as a range boundary for some species.

The 'Mid to Top North' pattern of movement is a continuation of the 'Mid Line North' pattern in that it includes the northern Australian coast. These species appear to largely vacate the northern extremes of their range during the tropical 'wet' season (i.e. southern summer).

The 'Towards North Inland and Coast' is a conglomerate of a number of patterns. Between the 'breeding' and 'over-wintering' quarters, these species move through the inland and, in some cases, along the coast towards the north. These species appear to flow into the northern tropical areas for their 'over-wintering' quarter. They appear to vacate the northern extremes of their range during the 'wet' season, which for most species is coincident with, or slightly after, their average breeding date. Additionally, two species in this group, the Sacred Kingfisher, *Todiramphus sanctus*, and the Olive-backed Oriole, *Oriolus sagittatus*, are likely to be intercontinental migrants, as their high population sum ratios

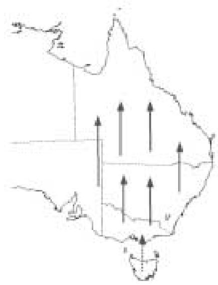
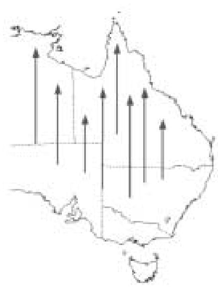
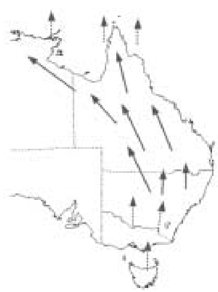
Pattern	Species	Map of Movement
Mid Line North 11 species	**Hoary-headed Grebe (*Poliocephalus poliocephalus*)** **Great Crested Grebe (*Podiceps cristatus*)** Great Cormorant (*Phalacrocorax carbo*) **Spotted Harrier (*Circus assimilis*)** **Swamp Harrier (*Circus approximans*)** **Little Button-quail (*Turnix velox*)** **Crimson Chat (*Ephthianura tricolor*)** **Orange Chat (*Ephthianura aurifrons*)** **Welcome Swallow (*Hirundo neoxena*)** **Tree Martin (*Hirundo nigricans*)** **Fairy Martin (*Hirundo ariel*)**	
Mid to Top North 12 species	**Australian Pelican (*Pelecanus conspicillatus*)** **White-faced Heron (*Egretta novaehollandiae*)** **Glossy Ibis (*Plegadis falcinellus*)** **Royal Spoonbill (*Platelea regia*)** **Yellow-billed Spoonbill (*Platelea flavipes*)** **Black Kite (*Milvus migrans*)** **Brown Falcon (*Falco berigora*)** **Nankeen Kestrel (*Falco cenchroides*)** **Australian Pratincole (*Stiltia isabella*)** **Red-backed Kingfisher (*Todiramphus pyrrhopygia*)** **Rainbow Bee-eater (*Merops ornatus*)** Little Woodswallow (*Artamus minor*)	
Towards North Inland and Coast 15 species	**Darter (*Anhinga melanogaster*)** **Little Egret (*Egretta garzetta*)** **White-necked Heron (*Ardea pacifica*)** **Great Egret (*Ardea alba*)** **Intermediate Egret (*Ardea intermedia*)** **Nankeen Night Heron (*Nycticorax caledonicus*)** **Straw-necked Ibis (*Threskiornis spinicollis*)** **Cockatiel (*Nymphicus hollandicus*)** **Sacred Kingfisher (*Todiramphus sanctus*)** **Striated Pardalote (*Pardalotus striatus*)** **White-throated (Gerygone *Gerygone olivacea*)** **Little Friarbird (*Philemon citreogularis*)** **Leaden Flycatcher (*Myiagra rubecula*)** **Olive-backed Oriole (*Oriolus sagittatus*)** Double-barred Finch (*Taeniopygia bichenovii*)	

Fig. 15. The North/South Inland patterns of movements. The species assigned these patterns appear to move predominantly in a north/south direction via inland routes. Species whose names are shown in bold had strong evidence for their movement classification and those not shown in bold had only suggestive evidence.

suggest their respective populations vary greatly in size.

Inland, non-cardinal-direction patterns

Over a dozen species appear, on average, to move in a north-north-west direction for the 'over-wintering' quarter in a pattern nominated as 'Slope Line' (Fig. 16). The direction of these movements appears to be appreciably different from directly north and thus are different from the cardinal directions. In particular, species in this group move away from the south-east regions in the winter in a direction that is almost perpendicular to the coast of New South Wales. This pattern of movement places the 'over-wintering' centroid of these species' ranges inland and northward of their 'breeding' centroids. For species with patchy range distributions maps, such as the Spotted Nightjar, *Eurostopodus argus*, and the Little Grassbird, *Megalurus gramineus*, this pattern is difficult to distinguish from other northward inland patterns, but it appears to be the closest depiction of the movements as illustrated by the maps and vectors.

At least five species, and possibly some listed under the 'Slope Line' and 'Towards North Inland and Coast' patterns, appear to take a more inland route on their southward return journey than on their northward journey. This results in these species displaying an approximately circular, anticlockwise pattern of movement. Unfortunately, this pattern traverses the 'Corner Country' region (where Queensland abuts South

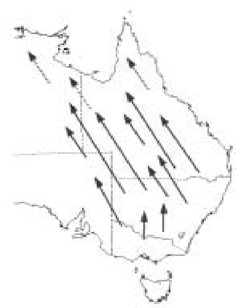
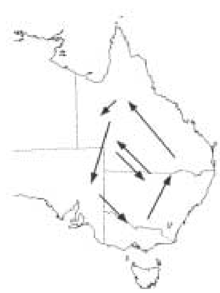
Pattern	Species	Map
Slope Line 14 species	**Australian Wood Duck (*Chenonetta jubata*)** **Little Black Cormorant (*Phalacrocorax sulcirostris*)** **Brown Goshawk (*Accipiter fasciatus*)** Little Eagle (*Hieraaetus morphnoides*) **Budgerigar (*Melopsittacus undulatus*)** Southern Boobook (Ninox novaeseelandiae) **Spotted Nightjar (*Eurostopodus argus*)** **Rufous Whistler (*Pachycephala rufiventris*)** **Black-faced Cuckoo-shrike (*Coracina novaehollandiae*)** **White-winged Triller (*Lalage sueurii*)** **White-breasted Woodswallow (*Artamus leucorynchus*)** **Masked Woodswallow (*Artamus personatus*)** **Clamorous Reed-Warbler (*Acrocephalus stentoreus*)** **Little Grassbird (*Megalurus gramineus*)**	
Inland Circle 5 species	**Pallid Cuckoo (*Cuculus pallidus*)** **Horsfield's Bronze-Cuckoo (*Chrysococcyx basalis*)** **White-browed Woodswallow (*Artamus superciliosus*)** **Rufous Songlark (*Cincloramphus mathewsi*)** **Brown Songlark (*Cincloramphus cruralis*)**	
Inland West-East (suspected) 1 species	**Black-chinned Honeyeater (*Melithreptus gularis*)**	

Fig. 16. The inland, non-cardinal-direction patterns of movement. The species listed with the 'Slope Line' pattern appear to move north-west away from south-eastern Australia. The species described by the 'Inland Circle' pattern appear to migrate north closer to the coast and return to the south via a more inland route. Species whose names are shown in bold had strong evidence for their movement classification and those not shown in bold had only suggestive evidence.

Australia) and this area is poorly represented in the Eastcoast database. It is therefore possible that this pattern is an anomaly arising from an interaction between the timing of surveys in these regions and the seasons. However, this pattern appears not just in the range map sequences, but also in each of these species' Centroid Vector diagrams. While these two measures are likely to be highly correlated, the size of each of these species' ranges and the generality of the vector diagrams should mask any local biases that may be influencing the visual interpretation of the range maps. This adds weight to the hypothesis that circular patterns of movement are present.

Finally, the Black-chinned Honeyeater, *Melithreptus gularis*, appears to be the sole example of a suspected 'Inland West/East' pattern of movement. Its range distribution maps clearly indicate at least two disjoint populations. Judging from the 'breeding' and 'over-wintering' range maps, the south-eastern population of this species appears sedentary. The north-western population, however, greatly increases in northern dry months (July quarter). This pattern of range variation is inconsistent with the patterns seen for intercontinental migrants. This presents the possibility that the excess of birds in the north-west originate from Western Australia and/or western Northern Territory, areas that have not been included in this study. The range maps given by Blakers *et al.* (1984), however, indicated that this is a realistic possibility. This species certainly warrants further investigation with the addition of data from the western half of Australia.

Local movement patterns

The species in the 'Local Movement Patterns' group are characterised by ranges that do not change significantly in their extents between periods but for which local variations were occurring in some restricted areas. For some species, extensions in the order of 200 km in one or more parts of their range were considered as local movements. For a number of range maps, it is difficult to differentiate between noise on the measurements (reporting rates) and genuine local variations in species density. This process becomes more difficult if the species' range includes the poorly surveyed areas of central and northern Australia.

While local patterns of movement were generally too varied or minor to warrant further sub-classification, a notable exception is listed in Fig. 17. The Forest Kingfisher appears to move towards the Queensland coast during its 'over-wintering' quarter and this pattern is also reported by Higgins (1999).

Confused movement patterns

In general, these 18 species (Table 4) were either cryptic, rare or occupied large ranges containing areas that are poorly represented by the atlas data. For these species it is apparent, however, that some type of movement is likely to be occurring. Nevertheless, the variations in the range maps are too great to be dismissed as noise and yet perceivable patterns do not emerge from the data. For example, the Black-eared Cuckoo Centroid Vector chart clearly indicates a north–south annual shift of some type by this species. However, the maps

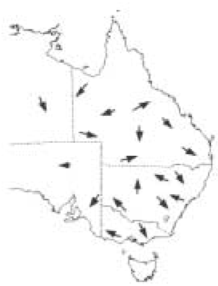
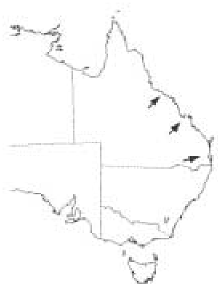
Pattern	Species	Map of Movement
Local Movements 39 species	Refer to the Appendix for listing. 17 Species had strong evidence supporting their movement classification	
QLD Inland to Coast 1 species	Forest Kingfisher (*Todiramphus macleayii*)	

Fig. 17. Local patterns of movement are exhibited by 39 species. One notable pattern within this grouping is that shown by the Forest Kingfisher, *Todiramphus macleayii*, which appears to move towards the Queensland coast during its 'over-wintering' quarter (16 June).

Table 4. Species that exhibit a confused pattern of movements
In general, these species are either cryptic, rare or occupy large ranges containing areas that are poorly surveyed. However, variations in their ranges suggest that some movements are occurring. Strong evidence was available to classify the species whose names are underlined as undertaking large-scale movements; only suggestive evidence was available for those species not underlined

Scientific name	Common name
Oxyura australis	Blue-billed Duck
Stictonetta naevosa	Freckled Duck
Lophoictinia isura	Square-tailed Kite
Hamirostra melanosternon	Black-breasted Buzzard
Falco subniger	Black Falcon
Falco peregrinus	Peregrine Falcon
Gallirallus philippensis	Buff-banded Rail
Cladorhynchus leucocephalus	Banded Stilt
Sterna nilotica	Gull-billed Tern
Chlidonias hybridus	Whiskered Tern
Chrysococcyx osculans	Black-eared Cuckoo
Tyto alba	Barn Owl
Pardalotus rubricatus	Red-browed Pardalote
Lichenostomus keartlandi	Grey-headed Honeyeater
Phylidonyris albifrons	White-fronted Honeyeater
Certhionyx pectoralis	Banded Honeyeater
Certhionyx niger	Black Honeyeater
Coracina maxima	Ground Cuckoo-shrike

of its range conceal the patterns of the movements as each map depicts a different variation of scattered sightings from which it is difficult to determine where movements are likely to be occurring.

Discussion

Possible sources of error

This study used data almost entirely observed, recorded, collated and vetted by volunteers. Can such a diverse collection of observers produce a usable data set of sufficient quality to warrant serious scientific investigation? Even amongst the scientific community, biases arising from observer variability or method variations are well documented (Kavanagh and Recher 1983; Shields and Recher 1984; Bell and Ferrier 1985). Consequently, when interpreting the results of the indicators presented above, one must first consider whether the effect seen is likely to be an error or artefact of the survey method. Errors and biases anticipated to present in the East-coast database, and their likely effects and significance on the analysis, are listed in Table 5.

When considering these potential sources of error or bias, it is critical to remember that the specific aim of our study was to detect changes in the reporting rates of species at a locality (or region) across months or seasons within a single ‘theoretical year’. Therefore, when considering the effects of potential error or biases upon our conclusions, the critical issue is: among the surveys conducted at this locality at this time of the year, which factors influence the likelihood of a species being recorded as present or absent during the survey? Furthermore, would such factors not also be operating at other sites and at other times of the year to which these data are being compared?

The case studies demonstrate that despite the large number of potential errors and biases, annual large-scale movements by Australian land-bird species can be detected and described using atlas-type data.

Movement indication statistics

Of all of the methods explored, the series of range distribution maps provide the most accessible but subjective evidence of bird movements. Large-scale migratory movements performed by a sizeable proportion of the population are readily apparent on the maps. As the proportion of the population involved in the movement decreases (e.g. contrast the Dollarbird and the Grey Fantail) or the movement becomes less uniform (e.g. the Budgerigar), the patterns of movement become less apparent.

Although a series of maps is readily interpretable, familiarity with the medium can elevate expectations of cartographic excellence that the data are inadequate to deliver. Earlier publication of these kinds of maps (Clarke *et al.* 1999) were rejected by some observers because they depicted very low species-reporting rates in regions where most observers regard the species as absent. If a doubting observer has never seen nor heard of that species in that region, and perhaps is presented with evidence to the contrary, the entire map sequence may be rejected out of hand as erroneous. While it is possible that what is depicted on the map is the result of an error, as discussed previously, many alternative explanations exist. A combination, or any one, of historical records, vagrants, aviary or farm escapees, the degree of data smoothing, legend colour selection, legend interval selection, coordinate precision and end-of-range definition could contribute to produce the effect deemed to be erroneous. Each one of these parameters involves subjective decisions relating to the level of their effects that should be tolerated. The most informative maps are likely to result from varying these parameters from species to species. For example, the edge of the Superb Lyrebird’s range may be set much closer to the ‘outermost’ sighting of the species than that of the Wedge-tailed Eagle. This is because range definition may be greatly influenced by the average area of the home-range size of each species. In a two-dimensional distribution, it is not always obvious when the outermost survey point becomes an outlier. The maps are a result of a series of decisions for which there is no one right answer.

Further complicating the interpretation of the maps is the coverage of the survey data. As previously mentioned, the variance of the reporting rate estimates increases as the number of surveys in an area decreases. As the survey coverage becomes sparser, mapping may not be possible at all.

Table 5. The major systematic errors anticipated to remain in the data used for this analysis
The errors are sorted by the estimated significance of their effects on the quality of the results

Bias or error	Effect	Significance of effect
Data-transcription errors	All data.	Errors likely to be distributed throughout the data, geographically and temporally.
Species-identification errors	Range size and reporting rate of particular species.	Small error in reporting rates of some species across range. Biased towards certain species, which may be categorised.
Mortality and natality	Reporting rate of all species. Not modelled and thus will appear as fluctuations.	Small error in reporting rates of all species across range. Larger errors in breeding areas.
Variation in species detection by observers	Range size and reporting rate of particular species.	Small underestimation in reporting rates of some species across range. Biased against cryptic species, which may be categorised.
Survey positional error	Range size and reporting rate for all species in survey	Moderate degradation of data across all species.
Reporting rate modelling density	Certain species likely to be poorly modelled, others adequately modelled.	Moderate error in density estimates of some species, which can be identified (Griffioen 2001).
Temporal variation in conspicuousness of species	Range size and reporting rate of particular species at certain times of year.	Moderate increase in variance of reporting rates of some species throughout year. Biased towards certain species which may be categorised.
Habitat variation in conspicuousness of species (Underhill *et al.* 1992)	Range size and reporting rate of various species in certain habitat types.	Moderate error biased towards certain habitats. Difficult to categorise.
Survey design bias for particular habitat types.	Range size and reporting rate of collections of species. Varies between databases.	Under- and over-estimation of reporting rates varying between databases. Likely to be significant for certain species (e.g. owls, waders).
Insufficient survey data	Range size and reporting rate of collections of species.	Incomplete data for many species significantly reduces power of analysis.
Observer preference for particular habitat types	Range size and reporting rate of collections of species. Varies from observer to observer.	Under- or over-estimation of reporting rates varying across range. Likely to be significant for many species.

This creates noisy areas and discontinuities on the maps, greatly reducing their utility. It is for this very reason that this study was restricted to the eastern half of Australia. The obvious solution to this problem is the addition of more survey data, targeted if possible, on areas of sparse coverage.

The population ratio proved very useful in flagging difficulties associated with species detection. Values close to unity, which indicate that the population size appears constant, can occur only if the species in question is not radically altering its behaviour during one period of the year, such that its detection is being affected, and the range of the species is evenly surveyed throughout the year. If either of these two criteria were not met, and the ratio was close to unity, then the population sums are being faithfully compensated by some other mechanism such as (a) natality/mortality, (b) seasonal changes in ease of detection of species, or (c) migration into and out of the survey area. These are less likely than the null hypothesis that nothing is occurring and in any case can, for the most part, be easily verified with the other indicators or by examination of the species' behaviour. Population ratios markedly different to unity indicate that one or more of these mechanisms must be occurring.

The population sums, as they are calculated in this study, are completely reliant on the robust and nearly linear relationship between reporting rate and density. This was verified by Griffioen (2001), with a very strong correlation between reporting rates and ABC-derived densities (median correlation coefficient $r = 0.856$, $n = 387$ species) using the models presented by Nachman (1981, 1984). However, as discussed previously, unresolved biases may still exist.

Syrjala's (1996) spatial statistics method provided a simple, robust and generally objective test for detecting changes in the distribution of species' ranges. Reinforcing the application of this technique was the correspondence of increasing statistical significance with more readily apparent changes in the quarterly range maps. This indicates that the statistic provides greater information than can be gleaned from its application to simple hypothesis testing. The test is not completely objective when applied to the atlas data as the selection of the grid size may affect the outcome of the test (Griffioen 2001). The test also lacks the facility to apply a variance estimate for each reporting rate. The noisy reporting rate estimates in remote areas certainly reduce the test's reliability. This affected each species uniquely such that comparisons of the degree of change between species could be misleading. While the test appears well designed to detect various combinations of range re-arrangements, a major limitation is its complete inability to detect an overall even decline or increase in the reporting rate of a species across its range. Such a change is nullified by the normalisation of the distributions. This is unfortunate as this test is otherwise well placed to detect range expansions and contractions occurring over extended periods rather than across one theoretical year.

The Centroid Vectors suggest movement patterns but this information is clouded by the method's generality. Movements specific to parts of a species' range are diluted across the whole range and this obscures their significance. In the worst case, movements occurring in one part of the range may be cancelled out by movements in other areas. The range map series greatly alleviates this problem by geographically identifying parts of the range in which changes may be occurring.

Large Movement Participation values and significant Centroid Vectors are both reliable indicators of migratory movements. Both of these statistics provide an indicator of the level of movement that may be occurring. These qualify Syrjala's Spatial Distribution Test. Obviously, these three statistical tests are likely to be highly correlated in that they use identical information in various mathematical combinations. It is not surprising therefore, that these statistics often support each other. However, a significant spatial-distribution test result along with a higher-than-average movement participation rate are not necessarily the result of a coordinated or cyclic movement in a given direction. The movements of many species are likely to be far too complex and localised to be reasonably described by a single, or series of, Centroid Vector(s). For many species, it would be useful to subdivide their range and determine regional statistics, data permitting.

Movements and patterns classification

The 37% (145/393) of species detected as undertaking movements agrees well with Rowley's (1975) estimate of 34%. However, it is low compared with Chan's (2001) estimate of 36%, when one considers that Chan's estimate was restricted to partial migrants and excluded full migrants and nomads.

The methods used to determine which species undertake large-scale movements illustrate the difficulty of categorising species into the traditional groups of 'migrant', 'partial migrant', 'nomad' and 'sedentary', especially since it is likely that we are imposing categories upon a continuum of movement patterns. For example, the range maps indicate that except for intercontinental migrants, none of the eastern Australian species in this study appear to be 'full' migrants (that is, species with geographically separate breeding and over-wintering areas). Thus, most birds in this study that were detected as undertaking movements are partial migrants or nomads. However, distinguishing these two groups is extremely difficult, as the primary trait separating migratory and nomadic movements is the coherence or synchrony of the movements and their repeatability. While the range maps do provide some information in this regard, these qualities are difficult to measure. As a result, both nomads and migratory species have been labelled as simply undertaking large-scale movements at some point throughout the year. Species for which no movements were detected were more easily categorised as sedentary. However, even this must be qualified by adding the phrase 'at the spatial resolution of this study'.

The classification of species into two levels of evidence, 'strong' and 'suggestive', effectively identifies those species for which more subjective decisions were employed to classify them as undertaking movements or being sedentary. This is because all species classified with 'suggestive evidence' relied heavily on the information interpreted from the range maps. However, if the nearly 100 species classified in this way were instead classified as 'unclear', the opportunity to explore the myriad of patterns present in these data would be greatly reduced. This demonstrates a limitation of the mathematical and statistical methods, which, in some cases, do not detect fluctuations that may be apparent in the maps. The cost of this power is that some species may be classified differently by other interpreters.

Intercontinental migrants exhibit rapid and synchronous long-distance movements that are likely to be correlated to their synchronous breeding times. The range map sequences of intercontinental migrants can be analysed to provide accurate timing as well as destination information. The population sums and Centroid Vectors provide supporting evidence. In many cases, however, the knowledge supplied by these techniques is not new. The real test of the value of these techniques lies in the promise of describing more subtle migratory patterns.

For intracontinental migrants, the degree of success in detecting their movements appears to be correlated to the participation rate of the population, the synchrony of the movement and the distance migrated. Vigorous migrants with a high participation rate, such as the Grey Fantail, were easily detected. Again, the map sequences of these species, especially multi-frame animated maps, provide accurate timing, source and destination information.

Many species migrating relatively short distances with low participation rates highlight the limit of sensitivity of these methods. As a result, some of these species only have 'suggestive evidence' of their movements, even though these movements are well documented by banding studies (e.g. Lane 1972). For species in well surveyed areas such as the Silvereye, *Zosterops lateralis* (Lane 1972) and the Flame Robin, *Petroica phoenicea* (Robinson 1992), increasing the resolution of the analysis may be all that is required to enable some of the movements of these species to be successfully described.

The statistics and maps are poorly placed to describe truly nomadic movements and irruptions because of the necessity to compress many years of data into one theoretical year in order to generate sufficient data for analysis. However, nomadic movements may contain a cyclical component of movement. Species whose movements track resources wherever and whenever they become available are at the mercy of those resources being replaced. The replacement of resources is likely to have a temporally cyclic pattern, but with great year-to-year variance. This explains the success of the statistical methods in detecting the cyclic movements of the Budgerigar and the Crimson Chat, *Epthianura tricolor*, which have been classified as nomads (Rowley 1975). The maps and the statistics of species such as these may fail to accurately describe these movements in any given year, but the pattern of movement may still be representative and useful. One must be extremely careful, however, that crucial and rarely repeated nomadic movements during some years are not discounted in the effort to generalise the pattern of movements. These rare movements may be critical to the survival of the species. This is a weakness of the data conglomeration approach used in this study. The compression of all of the atlas data into one theoretical year dilutes the coherence of irruptive and rarely repeated movement patterns. Only the sequential analysis of data from consecutive years, rather than the conglomeration of data across years, would allow such patterns to be detected. Currently, however, there are insufficient data to do this. Furthermore, given that nomadic species predominately occupy the drier regions of Australia, it is unlikely that there will ever be the human population base within these areas to support the collection of enough data to accurately model such movements within one year. Another possibility exists, and that is the analysis of the temporally coherent data to discern the frequency of a suite of occasionally repeating movement patterns. Such an analysis, however, would require decades of observations.

Some groupings of species are apparent in the patterns. Of the species within the 'coastal' patterns, 22 of 24 are forest-dwelling species, the exceptions being the Little Tern and the Cattle Egret. Not surprisingly, the inland-route migration patterns contain many open-range species such as raptors and chats along with some forest species. However, there were also a large number of species associated with water such as cormorants, grebes, ibis and herons. The migration of these species is likely to be highly dependent upon the inland rivers and lakes. These water resources, and their associated ecosystems, are coming under increasing pressure from water-intensive farming such as rice, cotton and fruit production. Identifying the essential elements, such as feeding, roosting and breeding sites, along these migratory routes should become a priority as obviously many species are dependent upon such resources in these semi-arid areas.

The circular pattern of movements at the edge of the interior of the country is perhaps the most interesting pattern of those described. All of the five species in this group are insectivorous and their breeding is centred around late October to early November. During breeding, these species predominantly occupy the southern parts of their ranges. After breeding, these species move northward towards their over-wintering areas, perhaps avoiding the interior of the country, which may still be too hot and dry. Around the 'over-wintering' quarter, they tend to move westward, which coincides with the interior of the country cooling. Between the 'over-wintering' and 'breeding' quarters, they undertake predominantly southerly migrations. The southern legs of these movements appear to be 100–400 km west of the northern legs. However, at this time, the interior of the country is cooler than when the northern legs were undertaken. In addition, the southern legs tend more south-easterly as breeding approaches and the interior heats up. Thus, a simple hypothesis for this pattern is that it has been shaped by temperature. It would be interesting to correlate the average regional temperatures along these routes with these species' reporting rates to determine whether a close relationship between these observations exists.

A wide variety of species were classified as having strong evidence of undertaking large-scale movements. The reliability of this classification is likely to have been closely related to the degree of movement undertaken. Species later classified as exhibiting local patterns of movements are more likely to be erroneously classified as non-sedentary than species that appear to undertake long-distance movements. The Superb Fairy-wren, *Malurus cyaneus*, is an interesting example of such a species. The Spatial Distribution Test suggests that significant variations in the distribution of this species occur during the year. Its range maps convincingly suggest that this variation is occurring only at the northern limit of its range. As a result, this species was classified as exhibiting 'local movements'. However, numerous studies of colour-banded individuals have indicated that the species is sedentary (Higgins *et al.* 2001). These variations in reporting rates in south-eastern Queensland may be the result of local movements, seasonal variation in the ability of observers to distinguish the Superb Fairy-wren from congeneric species also in eclipse plumage during the non-breeding season, or errors in the Eastcoast data. Many such examples are present in the results. For each of them, the answers to questions similar to those above will be varied. However, herein lies the power of the methods and results presented. For each species, the maps and the mathematical indicators may present evidence that is either contrary, or at least not part of, our current understanding of the movements and variations of distributions of that species. These tools can be used to form hypotheses and highlight potentially fruitful areas for further studies to enhance our understanding of the behaviours of these species.

A larger number of avian migratory patterns were apparent in the Australian east-coast atlas data than had been previously described (Keast 1968; Fullagar *et al.* 1986). The large-scale movement patterns detected agree well with Nix (1976). The 'Trans–Bass Strait' migrants and the eastern coastal patterns, in particular, faithfully follow the routes predicted by Nix (1976) for eastern Australia. This supports Nix's model of influence of environmental controls on the pattern of migratory movements in this region.

The 'North/South' inland patterns again agree well with Nix's (1976) predictions. Nix predicted that throughout inland Australia the dominant migratory direction would be north/south, which is present in most of these patterns. Nix (1976) did not predict, however, the significant westerly component that is apparent in the 'Towards North Inland and Coast', 'Slope Line' and 'Inland Circle' patterns (Figs 16, 17). The north-westerly 'breeding' to 'over-wintering' movement that defines these patterns is readily apparent in both the range maps and the Centroid Vectors of these 33 species. While Nix's map of predicted movements (Fig. 1) does predict north-west and south-east 'random' movements within the arid centre of Australia, the over-wintering flow towards the Northern Territory, western New South Wales and Queensland from the south-east is not implied. In the Mount Isa area (western Queensland) the movement directions indicated by the atlas data for some species are offset approximately 50° to the west of the north-north-east direction predicted by Nix. While it is recognised that the atlas data in the interior of the country are, in general, meagre, there is no reason to suspect that a considerable north-westerly bias has appeared in the 'over-wintering' range maps of half of the species undertaking large-scale migrations in eastern Australia. Such a bias is especially unlikely given that this north-westerly shift is apparent in a wide variety of avian families that make use of a variety of habitats, as recorded by many different observers.

The ecological processes producing these north-westerly patterns are not obvious. Indeed, verification of these patterns is necessary before hypotheses on the factors influencing them can be tested. Given the remote regions in which these suspected movements are occurring, it is unlikely that verification of these patterns will come from the chance recovery of banded birds. Studies specifically aimed at determining the origin of migrants over-wintering in western New South Wales, Queensland and eastern Northern Territory are required. It is likely that such studies would require remote tracking of individual birds, such as via satellite, in order to have any possibility of success.

The future

Once movement patterns have been identified in the data, as has been done in this study, it is likely that supplementary environmental information will reveal much about the controls and influences on the timing and pattern of migratory movements (e.g. Osborne and Tigar 1992; Robertson *et al.* 1994; Tobalske and Tobalske 1999). Further data sources could include bird band recoveries, and topographic, land-use, vegetation, fire-history and weather-mapping databases. The combination of such information and GIS software will enable the testing of a plethora of hypotheses on the movement patterns of Australia's avifauna. Such an integrated system would realise the full potential of the ecological information that lies hidden within the various avian databases.

This study examined the changes in the distributions of species' ranges over an annual time scale. The process of detecting range expansions, contractions and shifts due to habitat destruction over much longer time scales could use the same tools as those of this study. The value of atlas data will be amplified in time as human-induced changes occur across the Australian and global landscape. The atlas data will document the extent of the avian and ecological diversity that exists in Australia at this time. To appreciate the value of these data, one only has to dream of what comparative studies could now be performed if such a data set existed from the time of European settlement of Australia. How have species' densities changed since then? Have species' ranges contracted or expanded? What species were most affected by changes to the land and waterways in the last 200 years? Have migration patterns altered or perhaps halted? Do the changes identified reflect changes also experienced by other taxa? The answers to these questions may never be known as earlier data do not exist. However, these questions will still be as relevant in 200 years' time as they are today. At any time in the future, when these questions are asked again, the atlas data observed in the last 25 years will be a primary witness.

Conclusion

Notwithstanding the possible biases and errors described above, the results clearly indicate that atlas-type data are capable of providing vast amounts of information on the movements of birds throughout the east-coast of Australia. The case studies demonstrate that these data contain movement pattern and timing information that can be easily extracted and described. The further application of these tools to the hundreds of other species examined in thus study resulted in what was, for most of these species, the first analysis of their patterns of movement across most of their ranges. While these patterns have, for the most part, a general north–south alignment that has been described previously (Keast 1968; Lane 1972; Rowley 1975; Nix 1976; Blakers *et al.* 1984; Fullagar *et al.* 1986), the diversity of patterns apparent in eastern Australian migratory birds was not indicated by these earlier studies. As such, our knowledge of the movements of Australian birds has been significantly enhanced by the evidence that lies within the atlas and bird-count data.

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