# A long-term study of a Western Magpie *Gymnorhina tibicen dorsalis* population: group structure and demography

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The Australian Magpie *Gymnorhina tibicen* exhibits marked geographical variation in sociality and aspects of its demography. We conducted a 12-year investigation of a colour-banded population of Western Magpies *G. t. dorsalis* at Guildford, Western Australia to increase overall documentation and understanding of this variation; this report focuses on the composition of territorial groups and demography. Mean annual population density was 0.45 birds/ha and the mean annual adult sex ratio (males per female) at the start of the breeding season was 1.03. Emigration, immigration and within-population dispersal were all at relatively low levels. The main *identified* mortality agent of fledged individuals was collision with vehicles, but mean annual adult survival rates were high (~90% in both sexes). The most common numbers of adults in a territorial group were 1 and 4-7 males and 1 and 2 females, and many different combinations of numbers of adult males and females in a group were recorded within and among years. Magpies spent from 1-3 to 11-12+ years as a member of a group(s), but there was some adult membership change in a group in a mean of 80% of study years. The results showed some similarities to, and disparities with, the sociality and demography of magpie populations elsewhere in Australasia. The balanced *mean* adult sex ratio contrasted with the female-biased ratios typical of most bird species, although the ratio varied considerably among years. Both balanced and sex-biased adult sex ratios have been reported in other magpie populations. The considerable variation within and among groups in the numbers of adult male and female members resembled that recorded in other Australasian populations. The limited extent of intra- and inter-population dispersal contrasted markedly with that in many other magpie populations and could possibly reflect a relative lack of successful settlement options for dispersing individuals and/or a relatively high resource level in the natal area at Guildford. As in many other bird species, dispersal was female-biased, but male-biased dispersal has been recorded in the literature for another magpie population. The mean annual survival rate was very high in both sexes, which could reflect the low level of costly and risky dispersal recorded.

**Keywords:** Western Magpie; group composition; population size; sex ratio; survival and recruitment; dispersal

## INTRODUCTION

The Australian Magpie *Gymnorhina tibicen* occurs throughout much of the continent and part of Papua-New Guinea and has been introduced to New Zealand (Menkhorst *et al*. 2017). It is a generalist carnivore that inhabits open country with low ground cover and scattered trees, and has colonised many cities (Rollinson and Jones 2003). There are nine magpie subspecies, the most strongly sexually dichromatic ones being the Western Magpie *G. t. dorsalis* of south-western Western Australia and *G. t. papuana* of southern Papua-New Guinea (Schodde and Mason 1999).

Magpie sociality and demography vary strikingly among populations in various parts of Australasia. Most magpies defend all-purpose territories year-round (Robinson 1956; Carrick 1963; Veltman 1989; Farabaugh *et al*. 1992; Kallioinen *et al*. 1999; Hidayat 2018), but some populations also have non-territorial, non-breeding flocks of 'floaters' occupying apparently sub-optimal habitat (Carrick 1972; Veltman 1989; Hughes *et al*. 1996: Durrant and Hughes 2005). In northern Australia, territorial magpies occur mostly in socially monogamous pairs (Farabaugh *et al*. 1992; Hughes *et al*. 1996; Rollinson and Jones 2003), but in southern Australia and New Zealand territorial individuals mainly occur in groups containing various combinations of several adults of one or both sexes (Robinson 1956; Hughes *et al*. 1996; Veltman 1989; Farabaugh *et al*. 1992; Baker *et al*. 2000; Finn and Hughes 2001). Co-operative breeding (i.e. feeding of nestlings and fledglings by group members other than the likely parents) is negligible in some southern group-living populations (Veltman 1989; Brown and Farabaugh 1991) but common in others (Hughes *et al*. 1996; Finn and Hughes 2001; Pike *et al*. 2019). Dispersal of many young magpies from the natal territory is common in the first year of life in some south-eastern Australian populations (Durrant and Hughes 2005) and appears to be male-biased (Veltman and Carrick 1990; Toon 2007). However, it is negligible in some western populations, which are consequently more genetically distinct from one another than eastern ones (Baker *et al*. 2000).

The reasons for this variability in social organization and demography are not well understood. This motivated ER and IR in 1996 to initiate a long-term investigation of the (then) little-studied Western Magpie at Guildford, Western Australia (WA) to add to the overall documentation and understanding of the species' complex and variable sociality and population dynamics. The only substantial investigation of *G.t. dorsalis* up to that time had been by Robinson (1956) at Coolup, WA. However, subsequently there have been several further

**Figure 1.** *Aerial view of the Guildford study site showing the approximate location of group territories. Groups GG, JE and VM were included in the demographic analysis but not in that of group composition.*

investigations of various aspects of the behaviour, ecology and genetics of the Perth population that ER and IR studied (e.g. Hughes *et al.* 2003; Edwards *et al.* 2015; Ashton *et al.* 2018; Hidayat 2018; Pike *et al.* 2019).

Our findings on breeding and productivity in the Guildford study population have been reported previously (Rowley *et al.* 2022). The aim of the present paper is to document group composition and some demographic variables in the study population to facilitate comparison and integration with what is known about these aspects of magpie biology elsewhere in Australasia. In the current report, we pay special attention to theoretically significant demographic and social variables of the population, namely group composition, the sex ratio, dispersal and survival. Documenting adult sex ratios is important because they influence mate acquisition, sex roles, parental care regimes and population dynamics (Ancona *et al.* 2017). Dispersal affects *inter alia* the distribution of genetic diversity through space, inbreeding depression, cooperation and sociality and many life history traits (Ronce 2007). Documenting vital demographic rates, including annual survival, can be important in establishing and modelling population trends; for example, adult annual survival often has a particularly strong influence on the rate of population growth in long-lived species (Weiser *et al.* 2020).

## METHODS

### Study area

The 1996-2007 study was conducted in an ~200 ha area of the Perth, WA suburb of Guildford (-31º 53' 60" S, 115º 58' 22.8" E). The site is a residential area with housing, sporting facilities, parks and schools (Fig. 1). Annual rainfall in Guildford averages 865 mm and the mean maximum and minimum daily temperatures are 25ºC and 12ºC, respectively.

### Trapping and banding

Magpies caught in a baited, wire-mesh, ground trap were weighed (± 1 g), measured (wing chord and head-bill length ± 1 mm) and had their plumage characteristics recorded to age them retrospectively if they were immature and their fledging date was unknown (Rowley *et al.* in prep.). Adults are easily sexed in the field, males having a white back and females black back feathers with a white border (Menkhorst *et al.* 2017). Each adult was uniquely marked with stainless steel bands, one being numbered and one to three coloured; however, young birds were given expandable, plastic colour bands which were replaced with steel ones if they were later recaptured as adults. There was an initial, intense, broad-scale banding campaign throughout the study area from July-December 1966 and then the new cohort of juveniles in each group was caught and banded in March-April annually. Banding ceased in 2005, but population surveys continued until 2007. The banding program meant that throughout the study most magpies, except for some very young birds, were individually recognisable from a considerable distance using binoculars.

### Population surveys

Demographic data were obtained for all 16 territorial groups in the study area, but group composition was monitored intensively for 13 of these groups. Population density and sex

**Table 1**

Numbers of (a) adult males and females and (b) males and females of all ages post-fledging in studied Guildford Western Magpie groups from 1996-2007. Data are the number and rounded percentages of groups with various combinations of males and females (total n=172). To simplify the presentations, the numbers of groups with 4-7 adult and 5-9 immature males or 4-6 adult and 4-7 immature females are combined, as many of the possible combinations with larger numbers of males or females did not occur. The numbers highlighted in bold type are the most frequent (black font), second most frequent (red font) and third most frequent (blue font) combinations. The peripheral row and column percentages indicate the proportions of groups containing various numbers of males and females e.g. 29.1% of groups contained 1 adult female and 0-7 adult males and 38.4% of groups contained 1 adult male and 0-6 adult females.

**(a)**

| No. females | No. males | | | | | Percent of females |
|---|---|---|---|---|---|---|
| | 0 | 1 | 2 | 3 | 4-7 | |
| 0 | 1 (0.6) | 1 (0.6) | 1 (0.6) | 0 (0) | 0 (0) | *1.7* |
| 1 | 2 (1.2) | 19 (11.1) | 12 (7.0) | 10 (5.8) | 7 (4.1) | *29.1* |
| 2 | 0 (0) | **29 (16.9)** | 9 (5.2) | 4 (2.3) | 10 (5.8) | *30.2* |
| 3 | 2 (1.2) | **16 (9.3)** | **16 (9.3)** | 10 (5.8) | **12 (7.0)** | *26.7* |
| 4-6 | 0 (0) | 1 (0.6) | 5 (2.9) | 7 (4.1) | 8 (4.7) | *12.2* |
| *Percent of males* | *2.9* | *38.4* | *19.2* | *18.0* | *21.5* | *100* |

**(b)**

| No. females | No. males | | | | | Percent of females |
|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5-9 | |
| 1 | **15 (8.7)** | 8 (4.7) | 10 (5.8) | 1 (0.6) | 8 (4.7) | *24.4* |
| 2 | **18 (10.5)** | 8 (4.7) | 5 (2.9) | 6 (3.5) | 6 (3.5) | *25.0* |
| 3 | 8 (4.7) | **11 (6.4)** | **11 (6.4)** | 6 (3.5) | **15 (8.7)** | *29.7* |
| 4-7 | 1 (0.6) | 3 (1.7) | **11 (6.4)** | **11 (6.4)** | 10 (5.8) | *20.9* |
| *Percent of males* | *24.4* | *17.4* | *21.5* | *14.0* | *22.7* | *100* |

ratio and the size and composition of all the intensively studied groups were assessed annually at the start of the breeding season in August before recruitment of young of the year. With respect to group size and composition, we monitored one territorial group for 13 consecutive years, 10 groups for 12 years, one group for 10 years and one for 5 years (see Table 2 for details). Weekly surveys of all groups were made year-round, allowing us to closely monitor changes in composition and what caused them (mortality, immigration, emigration and within-population dispersal). Population mortality statistics were derived from our own observations of fatalities and reliable reports by the public. The high proportion of banded birds in the study population and continual monitoring of group composition allowed us to identify unbanded immigrants reliably.

*Data analysis*

Parametric analyses of variance (on transformed data) and non-parametric Wilcoxon and Chi-squared tests were used in analysing group residency and survival data.

## RESULTS

*Territorial groups*

a. Composition

It is important to note that although we obtained 172 annual records of group composition, they are not entirely independent because most groups were assessed in multiple years. Group composition (detailed in Table 1) can be summarised as follows:

1. The number of *adult males* in a group ranged from 0-7 and the most common numbers were one (38.4% of groups) and 4-7 (21.5% of groups).

2. The number of *adult females* in a group ranged from 0-6 and the most common numbers were two (30.2 % of groups) and one (29.1% of groups).

3. The most common *combinations of numbers of adult males and adult females* in groups were two females + one male (17% of groups) and 3 females + either 1 or 2 males (each 9.3% of groups).

4. The number of *adult plus immature males* in a group ranged from 1-9 and the most common numbers were one (24.4% of groups) and 5-9 (22.7% of groups).

5. The number of *adult plus immature females* in a group ranged from 1-7 and the most common numbers were 3 (29.7% of groups) and 2 (25% of groups).

6 The most frequently occurring *combinations of adult and immature males and females* were one male plus 2 females (10.5% of groups), one male plus one female and 5-9 males plus 3 females (each 8.7% of groups).

Almost half (45%) of the groups monitored had more adult females than adult males during any given year. Such an imbalance sometimes persisted in a group for several years and in one case six females attempted to breed in such a group (MM) in each of two years. Groups that had four or more adult males often acquired this number by retention of young males reared in the group. A few groups lacked an adult male or an adult female or in one case either of these members in a particular year. The latter case occurred in a newly-initiated group formed by immature birds in which breeding did not occur until a year after formation. Groups lacking an adult male were ones in which the resident male had disappeared, but

**Table 2**

Recruitment and losses in thirteen magpie groups at Guildford during the study period.

| Group | No. years monitored | Range in group size | No. (rounded %) of years with membership change | Mean (± SE) annual percentage of group composed of recruits | Total members lost during study | No. losses through mortality | No. losses through dispersal | No. losses due to unknown cause | Total recruits during study | No. of within-group recruits | No. of immigrant recruits |
|---|---|---|---|---|---|---|---|---|---|---|---|
| FP | 12 | 2-4 | 5 (46) | 10.6 (5.6) | 5 | 5 | 0 | 0 | 4 | 1 | 3 |
| MM | 12 | 6-11 | 11 (100) | 15.2 (4.2) | 12 | 9 | 3 | 0 | 15 | 14 | 1 |
| FM | 12 | 6-13 | 10 (91) | 13.6 (2.3) | 16 | 14 | 2 | 0 | 14 | 14 | 0 |
| HR | 12 | 9-13 | 10 (91) | 11.9 (3.9) | 12 | 12 | 0 | 0 | 14 | 14 | 0 |
| PG1 | 12 | 4-12 | 10 (91) | 27 (5.7) | 17 | 12 | 5 | 0 | 23 | 20 | 3 |
| HC | 12 | 4-8 | 11 (100) | 25.4 (6.3) | 13 | 12 | 1 | 0 | 18 | 17 | 1 |
| LP | 13 | 4-5 | 5 (42) | 7.5 (3.2) | 3 | 3 | 0 | 0 | 4 | 2 | 2 |
| NH | 12 | 6-11 | 9 (82) | 13.3 (3.9) | 9 | 7 | 0 | 2 | 11 | 11 | 0 |
| OV | 12 | 6-10 | 9 (82) | 9.8 (3.7) | 6 | 6 | 0 | 0 | 10 | 9 | 1 |
| SM | 12 | 3-7 | 10 (91) | 15.7 (5.8) | 11 | 11 | 0 | 0 | 10 | 10 | 0 |
| PG2 | 12 | 3-8 | 6 (55) | 11.5 (6.3) | 10 | 9 | 1 | 0 | 5 | 0 | 5 |
| WB | 10 | 2-7 | 9 (90) | 20.1 (4.3) | 12 | 8 | 4 | 0 | 10 | 10 | 0 |
| WS | 5 | 3-5 | 3 (75) | 18.3 (10.7) | 2 | 2 | 0 | 0 | 3 | 2 | 1 |

**Table 3**

Age/sex class of magpies lost from and recruited into thirteen Guildford groups during the study. Data are frequencies and (rounded percentages). SU = sex unknown.

| Age/sex | Losses | | Recruits | |
|---|---|---|---|---|
| | Died | Dispersed | Immigrated | Fledged in group |
| Adult male | 39 (36) | 2 (13) | 4 (22) | – |
| Adult female | 34 (31) | 5 (31) | 12 (67) | – |
| Immature male | 2 (2) | 1 (6) | 1 (6) | 30 (24) |
| Immature female | 1 (1) | 4 (25) | 0 (0) | 37 (30) |
| Immature SU | 34 (31) | 4 (25) | 1 (6) | 56 (46) |
| TOTAL | 110 | 16 | 18 | 123 |

**Table 4**

Duration of residency within groups. Data are number (and rounded percentage for that cohort) of banded birds of three categories that spent <1 to 12+ years resident in a group. Note that some birds were resident at different times in >1 group. Five unbanded birds, which were recognizable within a group because of plumage (young males) or some injury, are also included. M= male, F = female and U = unknown sex.

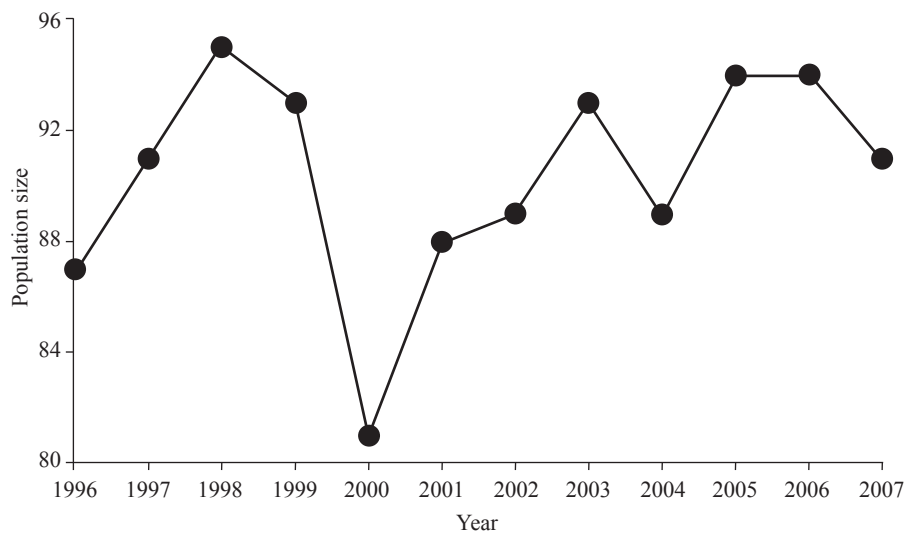| Years spent in a group | A. Birds banded as immatures or juveniles in natal territory, later lost from group and not detected in any other group | | | B. Known-age banded birds that were still present at end of present at end of study (2007) | | C. Birds banded as adults of unknown age that were still present at end of study | |
|---|---|---|---|---|---|---|---|
| | M | F | U | M | F | M | F |
| <1 | – | – | 11 (26) | – | – | – | – |
| 1-2 | 1 (4) | 7 (23) | 20 (48) | – | – | 1 (3) | 5 (18) |
| 2-3 | 6 (24) | 8 (26) | 11 (26) | 2 (7) | – | 5 (15) | 4 (14) |
| 3-4 | 4 (16) | 6 (19) | – | 3 (10) | 3 (11) | – | 5 (18) |
| 4-5 | 1 (4) | 5 (16) | – | 1 (4) | 3 (11) | 5 (15) | 3 (11) |
| 5-6 | 3 (12) | – | – | 8 (26) | 5 (18) | 4 (12) | 2 (7) |
| 6-7 | 2 (8) | 2 (7) | – | 5 (17) | 2 (7) | 3 (9) | – |
| 7-8 | – | 1 (3) | – | 3 (10) | 1 (4) | 1 (3) | 2 (7) |
| 8-9 | 5 (20) | 1 (3) | – | - | 3 (11) | 2 (6) | – |
| 9-10 | 2 (8) | – | – | 1 (4) | 5 (18) | 1 (3) | 1 (4) |
| 10-11 | – | – | – | 2 (7) | 2 (7) | – | – |
| 11-12 | 1 (4) | 1 (3) | – | 1 (4) | 4 (14) | – | – |
| 12+ | – | – | – | 3 (10) | - | 11 (33) | 6 (21) |
| n | | | | | | | |
| Total 216 | 25 | 31 | 42 | 29 | 28 | 33 | 28 |

**Figure 2.** *Annual variation in the number of magpies in the ~200 ha Guildford study area at the start of the breeding season from 1996-2007.*

**Table 5**

Dispersal of Guildford magpies to territories within and immediately adjacent to the study area. Sighting interval = number of days since disperser was last seen in original territory and first seen in new territory. Departure age is age when bird left original territory. Note that one female (RBYX) was involved in two dispersal events.

| Disperser identity | Sighting interval (days) | Departure age (months) |
|---|---|---|
| *Males:* | | |
| SYSX | 88 | 29 |
| YPYX | 10 | 27 |
| BYPX | 443 | 10 |
| RRXB | 255 | 10 |
| *Females:* | | |
| YRS | 35 | 72+ |
| YSS | 48 | 48 |
| VVRX | 54 | 36 |
| RBYX | 83 | 40 |
| RBYX | – | 89 |
| YGGX | 205 | 22 |
| GSYX | 173 | 17 |
| BVBX | 1 | 47 |
| YGBX | 21 | 20 |
| BVPX | 21 | 8 |
| YBPX | 458 | 21 |
| YYGX | 68 | 10 |
| YRXB | 259 | 10 |
| VBXB | 360 | 34 |
| YSXB | 35 | 14 |

breeding nonetheless occurred; we did not know if immature males sired the offspring in such groups, because extra-group paternity involving adult males could well have occurred (Hughes *et al.* 2003).

Thirteen magpie groups were monitored intensively for a total of 148 'group-years', group size varying within and among these groups from 2-13. Membership change and recruitment in these groups (summarized in Tables 2 and 3 and the yearly details given in Appendix 1) can be summarized as follows:

1. The mean percentage of study years in which there was some membership change in a particular group ranged from 42-100%, the grand mean being 79.5 ± 5.5%.

2. The mean annual percentage of a group that comprised recruits ranged from 7.5 to 27%, the grand mean being 15.4%.

3. The causes of the disappearance of 126 (of the total of 128) group members lost during this monitoring were presumed or known death (87.3%) and emigration from the study population (12.7%).

4. The recruitment of the 141 new group members that occurred during this study was mainly of within-group fledglings (87.9%), within-population dispersal from other groups in the study population having only a minor role (12.1%).

5. Adult males accounted for about one third of losses from groups and 36% of recorded presumed and known deaths, and adult females for 31% of both losses and recorded presumed and known deaths.

6. Immigrant adult males and females comprised respectively just 2.8% and 8.5% of group recruits; only 1.6% of immature recruits were immigrants, most being fledglings produced within the group.

b. Duration of residency

Magpies' duration of residency in groups (detailed in Table 4) can be summarised as follows:

1. For magpies whose *entire or minimal* period of residency in a group (or groups) was determined, the range in group residency duration was 1-3 to 11-12+ years.

2. For magpies for which the *entire* duration of group residency was determined (Column A, Table 4), 52% of males but only 16% of females spent > 5 years in group residency ($\chi^2_{(1)}$ = 8.164, P = .004).
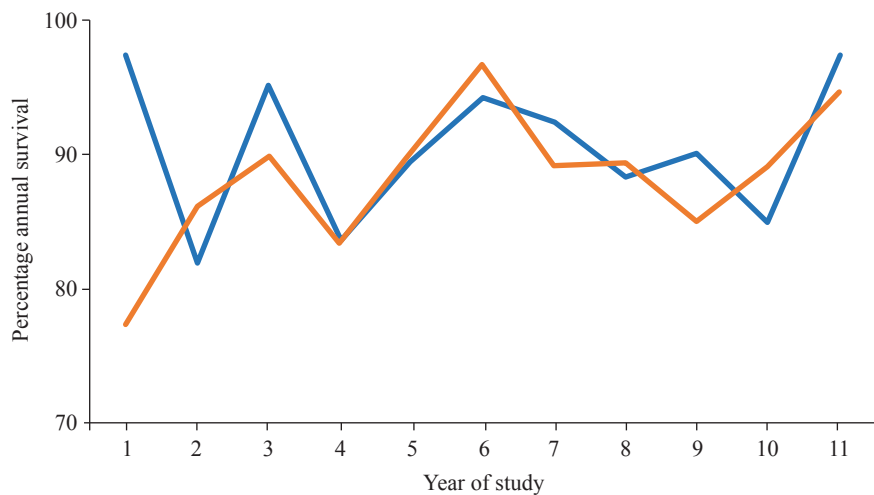
**Figure 3.** *Percentage annual survival of adult Western Magpies at Guildford 1996–2007. The Y axis extends only from 70-100% as all values fell in this range. Blue line is males, orange line is females. Survival was estimated as the percentage of birds alive at August 1 in one year that was still alive one year later. The number of birds alive at the start of the interval ranged from 35-44 for males and 29-40 for females. All marked birds ~ 2 years old or more included. Birds marked as juveniles included from the second year after hatching e.g. a bird hatched in 1996 was included from 1 Aug 1998 and scored as surviving to 1 Aug 1999 (or not).*

3. Similar percentages of males and females banded as fledglings that were still group residents at the end of the study (and hence whose complete group residency duration was not determined; Column B, Table 4) were known to have spent > 5 years in a group or groups (78 and 79%, respectively).

4. Among magpies banded as adults of unknown age that were still present at end of study (and hence whose entire group residency period was also not determined; Column C, Table 4), 66% of males and 39% of females spent > 5 years in group residency.

5. Approximate median group residency duration (including birds still resident at the end of the study) was 5-6 years for males and 4-5 years for females.

*Population density and sex ratio*

The mean number of magpies in the ~ 200 ha study area at the start of the breeding season over the 12-year study period was 90 (± 1.1) or ~0.45 birds per ha. Annual variation in population size was limited, the range being from 81-95 individuals (Fig. 2). The estimated mean annual sex ratio (males per female) in the population over the study period was 1.03 ± 0.031 (range 0.892-1.269) for adults and 1.21 ± 0.038 (range 0.048-1.471) for birds of all ages post-fledging.

*Dispersal*

i    Emigration from the study area

Only 3 of the 37 (8.1%) deaths of banded magpies recorded during the investigation occurred outside the study area; the fatalities occurred at distances of 800 m, 6 km and 8 km from the study site. One of these birds, a female, bred in the study area for 4 years before emigrating, another female emigrated within one year of fledging and a male resided in the study area for at least 4 years before departing. A further banded male was injured 5 km from the study site, resuscitated and released back into the study area, where it remained until its death.

ii.   Immigration into the study area

During the entire investigation only eight magpies (7 females and 1 male) immigrated into the study area and all became members of permanent groups. All except one of the females joined groups lacking a breeding female at the time and most or possibly all of them subsequently bred in their adopted group.

iii   Dispersal within the study area or its immediate surrounds

Within-population dispersal was observed during the study from a total of eight territories to a total of nine territories. During the entire investigation, only four males were recorded dispersing within the study area or its immediate surrounds (Table 5); they dispersed at 10-29 months post-fledging i.e. in Year 1-3 post-fledging. Fourteen females were recorded dispersing within the study site or its immediate surrounds (Table 5) and all moved to an immediately adjacent territory; they dispersed at 8-89 months post-fledging (mean 30 ± 6 mo. for exactly-aged birds) i.e. in Year 1-8 post-fledging. For these birds collectively, the sighting interval (i.e. period between the last sighting in the original and the first in the new territory) ranged from 1-443 days; we could not ascertain the interim location of dispersers who had very long sighting intervals. More dispersal occurred from July to October than from January to June.

*Mortality and survival*

Causes of magpie post-fledging mortality (n=36) that could be identified with certainty were: collision with vehicle (72.1%), injury or weakness/disease (11.2%), leg caught in wire (5.6%), entangled in fishing line (8.3%) and predation by birds (2.8%).
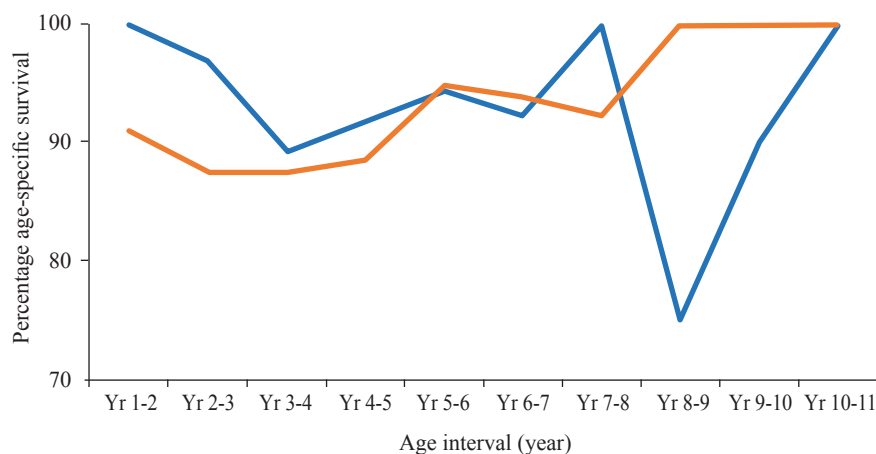
**Figure 4.** *Percentage age-specific survival of Western Magpies at Guildford 1996-2007. The Y axis extends from only 70-100% as all values fell in this range. Blue line shows males, orange line shows females. Survival estimated as the percentage of birds of known age and sex present on each 1 August that had not disappeared one year later. The numbers of males (blue) and females (orange) present at the start of each year (yr) (i.e. the sample sizes) were Yr 1-2 32, 44; Yr 2-3 32, 40; Yr 3-4 28, 32; Yr 4-5 25, 26; Yr 5-6 18, 19; Yr 6-7 13, 16; Yr 7-8 9, 13; Yr 8-9 8, 11; Yr 9-10 5, 6; Yr 10-11 2, 3.*

The *annual* survival rates (percentage of birds surviving through a specific calendar year) of adult magpies (i.e. 2 years old or more) over an 11-year period were similar for males (mean 90.6 %, range 82.2-97.4%) and females (mean 88.3%, range 77.4-96.8%) (N=11, Wilcoxon W= 24, P>.05) (Fig. 3). The *age-specific* survival rates (percentage of birds surviving through a given year of age) of male magpies did not change from 2 to 11 years of age ($F_{(1, 8)}$ =0.018, P=0.897) and averaged 93% (range 75-100%). Although female *age-specific* survival rates also averaged ~93% (range 88-100%), they increased with age ($F_{(1, 8)}$ =25.701, P<0.001) (Fig. 4); however, it is important to note that for females the sample size on which *age-specific* survival was based was quite small at older ages.

## DISCUSSION

### Group composition and residency

The adult composition (early in the breeding season) of 11% of studied territorial groups at Guildford comprised just one male and one female. Such a composition was characteristic of a more substantial proportion of groups in the Australian Capital Territory (ACT) (Carrick 1972) and New Zealand (Veltman 1984), but not of a majority. However, in southern Queensland the adult composition of the large majority of territorial groups comprised just a socially monogamous pair (Hughes *et al.* 1996; Rollinson and Jones 2003) (Table 6).

There was much variation in the adult composition of the 89% of Guildford groups that contained multiple adult males and/or multiple adult females, with one male + two females, one or two males + three females, and four to seven males + three females being the most common combinations. This sort of variation has also been recorded in the ACT (Carrick 1972), New Zealand (Veltman 1984) and Victoria (Finn and Hughes 2001), with sexual biases ranging from four times as many adult males as females to more than twice as many adult females as males (Table 6).

Guildford magpies spent from 1 to 12+ years as a resident in a group (or groups) during our study and it was common for members of both sexes to spend >5 years in group residency. There are few meaningful group residency statistics for other magpie populations because most studies have been too brief, but Carrick (1972) reported that ACT birds were commonly resident in a group for nearly four years (maximum 11 years) and Kaplan (2020) recorded a single 18-year residency in Melbourne. Thus, adult Western Magpies, like those elsewhere, typically had long periods of residency in one or more territorial groups.

### Population density and sex ratio

Population density of the entirely territorial Guildford population at the start of the breeding season averaged 0.45 magpies/ha and varied little annually. Reported mean densities for the territorial component of other Australasian populations range from 0.18 to 0.75 magpies/ha (Table 6), the closest value to that at Guildford being 0.3 birds/ha in south east Queensland where territorial groups were mostly socially monogamous pairs (Hughes *et al.* 1983). However, some populations also contain additional non-territorial, 'floater' flocks with densities of 0.5 to 1 bird/ha (Table 6), which would significantly increase the overall density of these populations (Carrick 1972; Veltman 1984). We did not accurately measure territory sizes at Guildford, but in other Australasian pair and group-based territorial populations/ sub-populations mean territory area varied from about 4-9 ha (Carrick 1972; Shurcliffe and Shurcliffe 1974; Hughes *et al.* 1983, 1996). Territoriality in magpies is probably concerned mainly with resource defence (Kaplan 2020), but the fact that territory size is not always positively correlated with group size within (e.g. Veltman 1989) or among (e.g. Hughes *et al.* 1996) populations indicates that the resource abundance-territoriality relationship may be complex in this species and requires further in-depth investigation.

**Table 6**

Summary values of some demographic and social metrics for Australian Magpie populations in various Australasian locations and the present study at Guildford, Western Australia.

| Metric | Source/locatioin | Values |
|---|---|---|
| *Population density (birds/ha)* | Carrick (1972): Canberra, ACT | 0.18 (territorial gps.) |
| | | 0.15 (flocks) |
| | Shurcliffe & Shurcliffe (1974): SA | 0.75 (territorial gps.) |
| | Veltman (1984): New Zealand | 0.7 (territorial gps.) |
| | | 1.0 (flocks) |
| | Hughes *et al.* (1983): South east Qld. | 0.3 (territorial groups) |
| | Present study: Guildford | 0.45 (territorial groups) |
| *Sex ratio (males per female)* | Carrick (1972): Canberra, ACT | 0.75 (permanent + marginal territorial groups) |
| | | 0.96 (mobile + open territorial groups) |
| | | 1.6 (flocks) |
| | Veltman (1984): New Zealand | 1 (territorial gps) |
| | | 0.5 to 1 (flocks) |
| | Finn & Hughes (2001): Seymour, Vic. | 0.89 (territorial gps.) |
| | Wood & Recher: (2004): Perth, WA | 40% adult males and 35% adult females in Kings Park population |
| | Pike (2019): Guildford, WA | 0.82 (territorial gps.) |
| | Present study: Guildford | 1.03 (territorial groups) |
| *Residency duration in groups* | Carrick (1972): Canberra, ACT | > 47 months, max. 133+ months |
| | Kaplan (2021): Melbourne, Vic. | 18 years (n=1) |
| | Present study: Guildford | Median: males 5-6 years, females 4-5 years. Some individuals for 11-12+ years |
| *Annual survival rate of adults (%)* | Carrick (1972): Canberra, ACT | Males 84; females 86 |
| | Veltman (1984): New Zealand | 85 (territorial gps.) |
| | | 90 (flocks) (daily survival rate) |
| | Present study: Guildford | Males 91; females 88 |
| *Most common adult group composition* | Carrick (1972): Canberra, ACT | 1 male + 1 female 47.3% |
| | | 1 male + 2 females 34.5% |
| | Veltman (1984): New Zealand | 2 males + 1 female 44% |
| | | 1 male + 1 female 22% |
| | Hughes et al. (1996): Mogill, Qld. | 1 male and 1 female 86% |
| | Finn & Hughes (2001): Seymour, Vic. | Highly variable, from equal numbers of males and females to 4x as many males as females to 2.3x as many females as males |
| | Rollinson (2003): South east Qld. | Predominantly 1 male and 1 female |
| | Durrant (2004): Rowsley, Vic. | 1 male + 2 females 56.3% |
| | | 1 or 2 males and 1-3 females 37.6% |
| | Present study: Guildford | 1 male and 2 females 17% |
| | | 1 or 2 males and 3 females 9% |
| | | Much variation |
| *Mortality agents* | Carrick (1972): Canberra, ACT | Road casualties (34.7%); various physical injuries and poisoning + shooting (16.3% each); disease (14.3%); predation (12.3%); electrocution (6.1%) (territorial birds, n= 49) |
| | Kaplan (2021): general summary | Predation (Wedge-tailed Eagle), road casualties, entanglement, diseases, poisoning, parasites, nutritional deficiencies |
| | Present study: Guildford | Road casualties (72%), entanglement (14%), injury/weakness disease (11%), predation by birds (3%) |
| *Dispersal* | Veltman (1984): New Zealand | 88% of surviving juveniles dispersed at 1 y.o., 6% at 2 y.o. and 6% remained as sub-adults |
| | Veltman & Carrick (1990): Canberra, ACT | Most dispersing juveniles settled on territory ≤ 1.6 km from natal site. 40% dispersed in Yr 1, 48% in Yrs 2-4 and 12% did not disperse (n=58). Males dispersed at younger age than females. Adults site-tenacious. |
| | Baker *et al.* (2001): multiple eastern sites | Genetic analysis implied some dispersal over much longer distances than reported by Veltman & Carrick (1990). |
| | Durrant & Hughes (2005): Rowsley, Vic. | In 2 seasons 59% and 63% of 1 y.o. and 29% and 57% of 2 y.o. birds dispersed. Dispersal male-biased in one season. |
| | Present study: Guildford | Emigration from and immigration into study population extremely limited. |
| | | Within-population dispersal: only 4 males and 15 females (usually to immediately adjacent territory) in entire 12-year study |

The mean annual adult sex ratio at Guildford over the study period was close to 1:1. The mean primary sex ratio at hatching was unknown, but in a large majority of bird species it is close to 1:1 (Donald 2007). If, as seems likely, this was also the case at Guildford, the balanced mean adult sex ratio would appear to suggest that the main factors thought to result in imbalanced avian adult sex ratios, namely sex differentials in mortality, maturation times and dispersal (Donald 2007; Szeleky *et al.* 2014; Ancona *et al.* 2017), were either negligible or somehow cancelled each other out in this population. However, adult males and females accounted for similar proportions of losses from the Guildford population due to known or reasonably presumed mortality, there is little evidence of a sex differential in maturation times (Rowley *et al.* in prep.) and dispersal from and into the population appeared to be limited (see also Baker *et al.* 2000). Therefore, sex differences in these three factors can possibly be ruled out as major influences on the observed balanced mean adult sex ratio at Guildford. Either the primary sex ratio or sex differential nestling mortality might conceivably have been significant influences on the mean adult sex ratio at Guildford, but both were impossible to determine by genetic sampling because of the inaccessibility of high nests.

The nearly balanced mean adult sex ratio of Guildford magpies contrasts with the sex ratio of a substantial majority of other bird species, which consistently have imbalanced, usually male-biased ratios (Mayr 1939; Donald 2007). Higher female mortality risks associated *inter alia* with longer dispersal and migration distances, a greater incubation effort and less efficient foraging are thought to cause these imbalanced adult sex ratios (Széleky *et al.* 2014). An important qualification and complication with respect to all the foregoing arguments about the provenance and rarity of the observed mean adult sex ratio at Guildford is that although overall it was balanced, it varied annually from male-biased to balanced to female-biased, so its principal drivers could conceivably have varied among years. Given that the mean adult sex ratio was ~1:1, the mean sex ratio of 1.21 for Guildford magpies *of all ages post-fledging* may indicate that mortality was greater among young males than young females.

Among group-living, territorial magpies elsewhere, the adult sex ratio varies from female-biased (Seymour, Victoria; Finn and Hughes 2001) to balanced (Linton, New Zealand; Veltman 1984) to male-biased (Kings Gardens, Perth; Wood and Recher 2004) (Table 6). Pike *et al.* (2019) reported a female-biased rather than a balanced adult sex ratio in our study population in a later investigation (Table 6); their study was of a much shorter duration and smaller scope, but adult sex ratios can vary over time in a population due to stochasticity (Széleky *et al.* 2014). Where magpie populations also contain a 'floater' flock, this obviously needs to be included in determining the overall population adult sex ratio, and estimated adult sex ratios for such flocks vary from male- or female-biased to balanced in various populations (Table 6). A male-biased adult sex ratio has sometimes been proposed as a prerequisite for the evolution of co-operative breeding (Donald 2007), but co-operative breeding occurred at Guildford where the mean adult sex ratio was approximately balanced and at Seymour, Victoria where it was female-biased (Finn and Hughes 2001).

*Dispersal*

Immigration into and emigration from the Guildford population were both at comparatively low levels. Dispersal within the study area was also limited: however, it was more common among females than males, occurred at a mean of 30 months post-fledging in females and usually involved moving to, and settling in, a territory immediately adjacent to the natal site. Genetic analysis is consistent with our observations of limited dispersal at Guildford in showing that south-western Australian magpie populations are more genetically distinct from one another than are eastern populations, indicating that inter-population gene-flow via dispersal is less pronounced in magpies in south-western than eastern Australia (Baker *et al.* 2000). The larger mean group size recorded for south–western than eastern populations is also consistent with lower juvenile dispersal rates (Baker *et al.* 2000).

The limited degree of dispersal at Guildford contrasts strongly with the high levels reported for some other group-living magpie populations. For example, more than 90% of juveniles dispersed from the natal territory at Linton, New Zealand (Veltman 1984) and in the ACT (Veltman and Carrick 1990), and dispersal of one and two–year olds was also at a high level at Rowsley, Victoria (Durrant and Hughes 2005). (Table 6). Dispersal is costly and risky (Ronce 2007), but avoidance of inbreeding and of competition with kin (including parents), heterosis and greater resource access are nonetheless thought to strongly favour natal dispersal in many species (Van Valen 1971; Greenwood 1980; Ronce 2007; Li and Kokko 2019). Therefore, the relatively low frequency of dispersal at Guildford might reflect a relative lack of opportunities for successful settlement and breeding by dispersing individuals in this area and/or a sufficiently high quality of resources in the natal area to dilute the disadvantages of philopatry. The genetic disadvantages of philopatry might be mitigated somewhat by the much higher level of extra-group paternity reported for this population than for some eastern group-living populations (Hughes *et al.* 2003).

Vertebrate dispersal is commonly sex-biased, the direction of the bias probably being influenced by local resource and mate competition (Greenwood 1980; Perrin and Mazalov 2000) and gender asymmetries (or 'handicaps') in morphology and parental care (Trochet *et al.* 2016). Female-biased dispersal predominates in birds (Greenwood 1980; Clarke *et al.* 1997; Mabry *et al.* 2013; Trochet *et al.* 2016; Li and Kokko 2019) and may have evolved because (a) familiarity with the local environment is more important to territorial, socially monogamous, resource-defending males than to females and hence favours male philopatry (Greenwood 1980) and (b) females are often smaller and less ornamented than males and thus dispersal is presumably less risky for them than for males (Trochet *et al.* 2016). Although dispersal was limited in Guildford magpies, it was female-biased. With respect to the gender asymmetries in morphology and parental care mentioned above: (a) although Western Magpies are sexually dichromatic they are not dramatically so, and consequently dispersal costs are unlikely to differ greatly between the sexes, and (b) although females performed considerably more parental care than males (Rowley *et al.* 2022) which theoretically should favour female

philopatry (Trochet *et al.* 2016), males were more philopatric. Therefore, morphological and parenting gender asymmetries are unlikely to have been drivers of female-biased dispersal in Guildford magpies: a greater importance of familiarity with local resources to males than females could potentially have been a significant factor promoting female-biased dispersal at Guildford, although the issue clearly requires further focused research.

*Mortality and survival*

The main identifiable post-fledging mortality agents for Guildford magpies, albeit based on a small sample size, were collisions with vehicles, injuries of unknown provenance and unidentified diseases. Carrick (1972) noted that road casualties, injuries, poisoning, shooting and diseases were the major causes of mortality in the ACT. Predation was insignificant at Guildford, but accounted for 12% of recorded fatalities of territorial individuals in the ACT (Table 6). There are few published quantitative records of magpie mortality and its causes for other Australasian locations.

The mean annual survival rate of adult magpies at Guildford was close to 90% in both sexes. This value is at the upper end of the reported range for Australian passerines (21-93%, Yom-Tov *et al.* 1992); this is perhaps unsurprising, as the species is among the heavier members of this order in Australia (215-360 g; Menkhorst *et al.* 2017) and annual survival of Australian and other passerines is positively correlated with body mass (Dobson 1990; Yom-Tov *et al.* 1992). The only other published annual survival rate for magpies of which we are aware (apparently drawn from composite nationwide Australian Bird and Bat Banding Schemes records; Yom-Tov *et al.* 1992) is much lower (67%). Although the sample from which the latter value was derived could conceivably have included some Western Magpie records, the disparity is nonetheless striking. We speculate that the higher survival rate at Guildford could reflect the much lower rate of risky dispersal in western than eastern magpies (Baker *et al.* 2000; this study) and possibly a relatively higher resource level on Guildford group territories that promoted philopatry. Rowley and Russell (1991) argued that the annual survival rates of adult south temperate land birds are higher than those of north temperate counterparts because the comparatively stable environment on the south temperate land mass may promote greater longevity and favour a slower breeding strategy. However, whilst the mean adult annual survival rate of Guildford magpies was much greater than those of most north temperate passerines (40-60%; Karr *et al.* 1990), the rate of 67% cited above for Australian Magpies in general is not.

Survival rate in most bird species is lower in young and very old individuals (Robinson 2010; Muñoz *et al.* 2018), probably due to juveniles' lack of proficiency in predator-avoidance, foraging, competition and time-energy budgeting (Wunderle 1991) and old birds' senescence. Female magpie survival rates at Guildford did increase with age from 2-11 years old as predicted by theory, although this could have been an artefact of the small number of females present in later years. However, the survival rates of male magpies did not change significantly with age, although our data did not encompass as many as possibly the last 9+ years of the lifespan of many males and so may not have adequately captured a possible decrease in annual survival of old individuals.

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## APPENDIX 1

Annual changes in composition of thirteen magpie groups at Guildford, 1996-2007. Losses shown in red, recruits in black (column 4). In column 3, AM = adult male (blue), AF = adult female (brown), IM = immature male (orange), IF = immature female (green), ISU = immature of unknown sex (purple). In column 4, disp = dispersed within study population, immig = immigrated into study population, emig = emigrated from study population and wgr = within-group recruit.

| Group | Year(s) \ (group size) | Composition | - Losses<br>+ Recruits | Proportion comprising recruits |
|---|---|---|---|---|
| FP | 1996-2000<br>(4) | 3 AM (BBB, SGS, YRR)<br>1 AF (GYB) | | 0 in 1997-2000 |
| | 2001<br>(3) | 2 AM (SGS, YRR)<br>1 AF (GS) | - 1 AM (BBB), 1 AF (GYB) (both died)<br>+ 1 AF (GS) (immg) | 0.333 |
| | 2002<br>(2) | 1 AM (YYR)<br>1 AF (GS) | - 1 AM (SGS) (died) | 0 |
| | 2003<br>(2) | 1 AM (YRR)<br>1 AF (GS) | No change | 0 |
| | 2004<br>(4) | 1 AM (YRR)<br>2 AF (GS, BV)<br>1 IF (SR) | + 1 AF (BV) (immg), 1 IF (SR) (wgr) | 0.5 |
| | 2005<br>(2) | 1 AM (YYR)<br>1 AF (BV) | -1 AF (GS), 1 IF (SR) (both died) | 0 |
| | 2006<br>(3) | 1 AM (YYR)<br>1 AF (BV)<br>1 IM (04) | +1 IM (04) (prob immg) | 0.333 |
| | 2007<br>(3) | 2 AM (YYR, 04)<br>1 AF (BV) | No change | 0 |
| MM | 1996<br>(6) | 2 AM (BBS, VYY)<br>3 AF (VBR, YGB, RVV)<br>1 IM (GGS) | | |
| | 1997<br>(10) | 2 AM (BBS, VYY)<br>2 AF (VBR, YGB)<br>4 IM (YYR, RRB, L, GGS)<br>1 IF (VRY)<br>1 ISU (BYR) | -1 AF (RVV) (died)<br>+ 3 IM (YYR, RRB, L), 1 IF (VRY) (all wgr), 1 ISU (immg) | 0.5 |
| | 1998<br>(9) | 3 AM (VYY, GGS, L)<br>3 AF (VBR, YGB, VRY)<br>2 IM (YYR, RRB)<br>1 ISU (BYR) | -1 AM (BBS) (died) | 0 |
| | 1999<br>(9) | 4 AM (YYR, RRB, L, VYY)<br>3 AF (VBR, YGB, VRY)<br>1 IF (SG)<br>1 ISU (YB) | -1 AM (GGS), 1 ISU (BYR) (both died)<br>+ 1 IF (SG), 1 ISU (YB) (both wgr) | 0.222 |
| | 2000<br>(9) | 4 AM (YYR, RRB, L, VYY)<br>4 AF (VBR, YGB, VRY, SG)<br>1 IF (PY) | -1 ISU (YB) (died)<br>+ 1 IF (PY) (wgr) | 0.111 |
| | 2001<br>(10) | 4 AM (YYR, RRB, L, VYY)<br>5 AF (VBR, YGB, VRY, SG, PY)<br>1 IF (GR) | + 1 IF (GR) (wgr) | 0.1 |
| | 2002<br>(11) | 4 AM (YYR, RRB, L, VYY)<br>6 AF (VBR, YGB, VRY, SG, PY, GR)<br>1 ISU (BY) | + 1 ISU (BY) (wgr) | 0.091 |
| | 2003<br>(10) | 3 AM (YYR, L, VYY)<br>6 AF (VBR, YGB, VRY, SG, PY, GR)<br>1 ISU (BY) | - 1 AM (RRB), 1 ISU (BY) (both disp)<br>+ 1 IF (YY) (wgr) | 0.1 |
| | 2004<br>(10) | 3 AM (YYR, L, VYY)<br>5 AF (VBR, YGB, VRY, SG, PY)<br>1 IM (BY)<br>1 IF (GG) | -1 AF (GR) (died), 1 IF (YY) (disp)<br>+ 1 IM (BY), 1 IF (GG) (both wg r) | 0.2 |
| | 2005<br>(9) | 2 AM (L, VYY)<br>6 AF (VBR, YGB, VRY, SG, PY, GG)<br>1 IM (BY) | -1 AM (YYR) (died) | 0 |
| | 2006<br>(8) | 3 AM (L, VYY, BY)<br>4 AF (VBR, YGB, VRY, SG)<br>1 ISU (05) | -2 AF (GG, PY) (both died)<br>+ 1 ISU (05) (wgr) | 0.25 |
| | 2007<br>(9) | 3 AM (L, VYY, BY)<br>4 AF (VBR, YGB, VRY, SG)<br>2 ISU (05, 06) | + 1 ISU (06) (wgr) | 0.1 |
| FM | 1996<br>(10) | 5 AM (RGB, RYR, YSR, RRG, SYG)<br>4 AF (BSB, SSS, RGR, GBY)<br>1 IM (BRG) | | |

| Group | Year(s) \ (group size) | Composition | - Losses<br>+ Recruits | Proportion comprising recruits |
|---|---|---|---|---|
| | 1997 (11) | 5 AM (RGB, RYR, YSR, RRG, SYG)<br>3 AF (BSB, SSS, RGR)<br>1 IM (BRG)<br>1 IF (BVR)<br>1 ISU (YVY) | -1 AF (GBY) (died)<br>+ 1 IF (BVR), 1 ISU (YVY) (both wgr) | 0.182 |
| | 1998 (11) | 4 AM (RGB, RYR, YSR, SYG)<br>4 AF (BSB, SSS, RGR, BVR)<br>1 IM (BRG)<br>2 IF (VRG, RBY) | -1 AM (RRG), 1 ISU (YVY) (both died)<br>+ 2 IF (VRG, RBY) (both wgr) | 0.182 |
| | 1999 (13) | 5 AM (RGB, RYR, YSR, SYG, BRG)<br>5 AF (BSB, SSS, BVR, VRG, RBY)<br>1 IF (YG)<br>2 ISU (PP, BY) | -1 AM (RGR) (died)<br>+ 1 IF (YG), 2 ISU (PP, BY) (all wgr) | 0.231 |
| | 2000 (11) | 3 AM (RYR, YSR, BRG)<br>6AF (BSB, SSS, BVR, VRG, RBY, YG)<br>2 ISU (PP, BY) | -2 AM (RGB, SYG) (both died) | 0 |
| | 2001 (7) | 3 AM (RYR, YSR, BRG)<br>3 AF (BSB, SSS, VRG)<br>1 IF (BB) | -3AF (BVR, YG, RBY) (one died, 2 disp), 2 ISU (PP, BY)<br>(both died)<br>+ 1 IF (BB) (wgr) | 0.143 |
| | 2002 (8) | 3 AM (RYR, YSR, BRG)<br>4 AF (BSB, SSS, VRG, BB)<br>1 IF (YY) | + 1 IF (YY) (wgr) | 0.125 |
| | 2003 (6) | 2 AM (RYR, BRG)<br>2 AF (VRG, YY)<br>1 IM (BR) | -1 AM (YSR), 3 AF (BSB, SSS, BB) (all died)<br>+ 1 IM (BR), 1 IF (RY) (both wgr) | 0.2 |
| | 2004 (6) | 1 AM (RYR)<br>3 AF (VRG, YY, RY)<br>1 IM (BR)<br>1 IF (PB) | -1 AM (BRG) (died)<br>+ 1 IF (PB) (wgr) | 0.167 |
| | 2005 (7) | 2 AM (RYR, BR)<br>4 AF (VRG, YY, RY, PB)<br>1 IM (SV) | + 1 IM (SV) (wgr) | 0.143 |
| | 2006 (7) | 2 AM (RYR, BR)<br>4 AF (VRG, YY, RY, PB)<br>1 IM (SV) | No change | 0 |
| | 2007 (8) | 2 AM (RYR, BR)<br>4 AF (VRG, YY, RY, PB)<br>1 IM (SV)<br>1 ISU (07) | + 1 ISU (07) (wgr) | 0.125 |
| HR | 1996 (9) | 4 AM (BYY, GYS, VVB, RRY)<br>3 AF (YSY, GX, GSS)<br>2 IM (YGY, BGB) | | |
| | 1997 (11) | 5 AM (BGB, BYY, GYS, VVB, RRY)<br>3 AF (YSY, GX, GSS)<br>1 IM (YGY)<br>1 IF (YVR)<br>1 ISU (BRY) | + 1 IF (YVR), 1 ISU (BRY) (both wgr) | 0.182 |
| | 1998 (12) | 5 AM (BYY, GYS, YGY, VVB, RRY)<br>3 AF (YSY, GSS, YVR)<br>4 IM (RVS, GYR, YBB, SYB) | -1 AM (BGB), 1 AF (GX), 1 ISU (BRY) (all died)<br>+ 4 IM (YBB, RVS, GYR, SYB) (all wgr) | 0.417 |
| | 1999 (13) | 4 AM (BYY, GYS, VVB, RRY)<br>2 AF GSS, YVR)<br>5 IM (GP, RVS, GYR, YBB, SYB)<br>1 IF (BB)<br>1 ISU (YS) | -2 AF (YSY, YGY) (both died)<br>+ 1 IF (BB), 1 IM (GP), 1 ISU (YS) (all wgr) | 0.231 |
| | 2000 (12) | 4 AM (BYY, GYS, VVB, RRY)<br>2 AF (YVR, BB)<br>5 IM (GP, RVS, GYR, YBB, SYB)<br>1 ISU (YS) | -1 AF (GSS) (died) | 0 |
| | 2001 (10) | 6 AM (BYY, GYS, RVS, GYR, SYB, YBB)<br>2 AF (YVR, BB)<br>1 IM (GP)<br>1 IF (BP) | -2 AM (VVB, RRY), 1 ISU (YS) (all died)<br>+ 1 IF (BP) (wgr) | 0.1 |
| | 2002 (10) | 7 AM (BYY, GYS, RVS, GYR, SYB, YBB, GP)<br>3 AF (YVR, BB, BP) | No change | 0 |
| | 2003 (11) | 7 AM (BYY, GYS, RVS, GYR, SYB, YBB, GP)<br>3 AF (YVR, BB, BP)<br>1 IF (BY) | + 1 IF (BY) (wgr) | 0.091 |
| | 2004 (10) | 7 AM (BYY, GYS, RVS, GYR, SYB, YBB, GP)<br>3 AF (YVR, BB, BY) | -1 AF (BP) (died) | 0 |

| Group | Year(s) \ (group size) | Composition | - Losses<br>+ Recruits | Proportion comprising recruits |
|---|---|---|---|---|
| | 2005<br>(10) | 6 AM (BYY, GYS, RVS, GYR, SYB, YBB)<br>3 AF (YVR, BB, BY)<br>1 IM (RY) | + 1 IM (RY) (wgr) | 0.1 |
| | 2006<br>(11) | 5 AM (RVS, GYR, YBB, BYY, GYS)<br>3 AF (YVR, BB, BY)<br>1 IM (RY)<br>2 ISU (07, 08) | -1 AM (SYB) (died)<br>+ 2 ISU (07, 08) (both wgr) | 0.182 |
| | 2007<br>(10) | 5 AM (RVS, GYR, BYY, GYS, RY)<br>3 AF (YVR, BB, BY)<br>2 ISU (07, 08) | -1 AM (YBB) (died) | 0 |
| PG1 | 1996<br>(7) | 1 AM (SGG)<br>3 AF (RYB, YRS, YSS)<br>2 IM (YYV, YSG)<br>1 ISU (GBR) | | |
| | 1997<br>(9) | 1 AM (SGG)<br>3 AF (RYB, YRS, YSS)<br>3 IM (RVY, YYV, YSG)<br>1 IF (VVR)<br>1 ISU (GBR) | + 1 IM (RVY), 1 IF (VVR) (both wgr) | 0.222 |
| | 1998<br>(9) | 3 AM (SGG, YSG, YYV)<br>4 AF (RYB, YRS, YSS, VVR)<br>1 IM (RVY)<br>1 ISU (BBS) | -1 ISU (GBR) (died)<br>+ 1 ISU (BBS) (wgr) | 0.111 |
| | 1999<br>(7) | 4 AM (SGG, YSG, YVV, RVY)<br>1 AF (RYB)<br>2 ISU (BS, PG) | -3 AF (YRS, VVR, YSS) (emig), 1 ISU (BBS) (died)<br>+ 2 ISU (PG, BS) (both wgr) | 0.286 |
| | 2000<br>(4) | 1 AM (YSG)<br>3 AF (BG, PS, BR) | -3 AM (RVY, YYV, SGG), 1 AF (RYB), 2 ISU (PG, BS) (all died)<br>+ 3 AF (BG, PS, BR) (all immig) | 0.75 |
| | 2001<br>(5) | 1 AM (YSG)<br>3 AF (BG, PS, BR)<br>1 ISU (SY) | + 1 ISU (SY) (wgr) | 0.2 |
| | 2002<br>(8) | 1 AM (YSG)<br>3 AF (BG, PS, BR)<br>2 IM (GG, RY)<br>2 ISU (YB, SY) | + 2 IM (GG, RY), 1 ISU (YB) (all wgr) | 0.375 |
| | 2003<br>(9) | 1 AM (YSG)<br>3 AF (BG, PS, BR)<br>4 IM (RB, BS, GG, RY)<br>1 ISU (SR) | -2 ISU (YB, SY) (one disp, one died)<br>+ 2 IM (RB, BS), 1 ISU (SR) (all wgr) | 0.333 |
| | 2004<br>(9) | 1 AM (YSG)<br>3 AF (BG, PS, BR)<br>4 IM (RB, BS, GG, RY)<br>1 ISU (YG) | -1 ISU (SR) (died)<br>+ 1 ISU (YG) (wgr) | 0.111 |
| | 2005<br>(12) | 3 AM (YSG, RY, GG)<br>3 AF (BG, PS, BR)<br>2 IM (RB, BS)<br>2 IF (VB, BY)<br>2 ISU (VR, YW) | - 1 ISU (YG) (died)<br>+ 2 IF (VB, BY), 2 ISU (VR, YW) (all wgr) | 0.333 |
| | 2006<br>(11) | 5 AM (YSG, RY, GG, BS, RB)<br>5 AF (BG, PS, BR, VB, BY)<br>1 ISU (09) | -2 ISU (VR, YW) (one died, one disp)<br>+ 1 ISU (09) (wgr) | 0.091 |
| | 2007<br>(13) | 5 AM (YSG, RY, GG, BS, RB)<br>5 AF (BG, PS, BR, VB, BY)<br>3 ISU (09, 010, 011) | + 2 ISU (010, 011) (wgr) | 0.154 |
| HC | 1996<br>(4) | 1 AM (GRG)<br>3 AF (YBR, BGY, BGG) | | |
| | 1997<br>(4) | 1 AM (GRG)<br>2 AF (YBR, BGG)<br>1 IF (RSV) | -1 AM (BGY) (died)<br>+ 1 IF (RSV) (wgr) | 0.25 |
| | 1998<br>(5) | 1 AM (SYS)<br>3 AF (YBR, RSV, BGG)<br>1 ISU (VSY) | - 1 AM (GRG) (died)<br>+ 1 AM (SYS) (immig), 1 ISU (VSY) (wgr) | 0.4 |
| | 1999<br>(7) | 1 AM (SYS)<br>3 AF (YBR, RSV, BGG)<br>1 IF (YY)<br>2 ISU (GG, PS) | -1 ISU (VSY) (died)<br>+ 1 IF (YY), 2 ISU (GG, PS) (all wgr) | 0.429 |
| | 2000<br>(6) | 1 AM (SYS)<br>3 AF (RSV, BGG, YY)<br>2 ISU (SB, GG) | -1 AM (YBR) (died)<br>+ 1 ISU (SB) (wgr) | 0.167 |

| Group | Year(s) \ (group size) | Composition | - Losses <br> + Recruits | Proportion comprising recruits |
|---|---|---|---|---|
| | 2001 (8) | 2 AM (SYS, YY) <br> 1 AF (RSV) <br> 1 IM (PV) <br> 3 IF (VS, BV, YB) <br> 1 ISU (YP) | -1 AF (BGG), 2 ISU (SB, GG) (all died) <br> + 1 IM (PV), 3 IF (VS, BV, YB), 1 ISU (YP) (all wgr) | 0.625 |
| | 2002 (7) | 3 AM (SYS, YY, PV) <br> 4 AF (RSV, VS, BV, YB) | -1 ISU (YP) (died) | 0 |
| | 2003 (6) | 3 AM (SYS, YY, PV) <br> 3 AF (RSV, VS, BV) | -1 AF (YB) (died) | 0 |
| | 2004 (7) | 3 AM (SYS, YY, PV) <br> 3 AF (RSV, VS, BV) <br> 1 ISU (RG) | + 1 ISU (RG) (wgr) | 0.143 |
| | 2005 (6) | 3 AM (SYS, YY, PV) <br> 2 AF (RSV, VS) <br> 1 ISU (RG) | -1 AF (BV) (disp) | 0 |
| | 2006 (5) | 1 AM (YY) <br> 2 AF (RSV, VS) <br> 2 IM (12, 13) | -2 AM (PV, SYS), 1 ISU (RG) (all died) <br> +2 IM (12, 13) (both wgr) | 0.4 |
| | 2007 (8) | 1 AM (YY) <br> 2 AF (RSV, VS) <br> 2 IM (12, 13) <br> 3 ISU (14. 15. 16) | + 3 ISU (14, 15, 16) (all wgr) | 0.375 |
| LP | 1995 (4) | 1 AM (RRR) <br> 2 AF (YBY, RSG) <br> 1 IF (SBS) | | |
| | 1996 (5) | 1 AM (RRR) <br> 3 AF (YBY, RSG, SBS) <br> 1 IM (GYG) | + 1 IM (GYG) (wgr) | 0.2 |
| | 1997 – 1998 (both 5) | 1 AM (RRR) <br> 3 AF (YBY, RSG, SBS) <br> 1 IM (GYG) | No change | 0 in 1997 & 1998 |
| | 1999 (5) | 2 AM (RRR, GYG) <br> 3 AF (YBY, RSG, SBS) | No change | 0 |
| | 2000 (4) | 1 AM (GYG) <br> 3 AF (YBY, RSG, SBS) | - 1 AM (RRR) (died) | 0 |
| | 2001-2003 (4) | 1 AM (GYG) <br> 3 AF (YBY, RSG, SBS) | No change | 0 in 2001 & 2003 |
| | 2004 (4) | 2 AM (GYG, RRB) <br> 2 AF (YBY, RSG) | -1 AF (SBS) (died) <br> + 1 AM (RRB) (immig) | 0.25 |
| | 2005 (4) | 2 AM (GYG, RRB) <br> 2 AF (RSG, U20) | -1 AF (YBY) (died) <br> + 1 AF (U20) (immig) | 0.25 |
| | 2006 (4) | 2 AM (GYG, RRB) <br> 2 AF (RSG, U20) | No change | 0 |
| | 2007 (5) | 2 AM (GYG, RRB) <br> 2 AF (RSG, U20) <br> 1 ISU (U21) | + 1 ISU (U21) (wgr) | 0.2 |
| NH | 1996 (7) | 2 AM (YYY, BRR) <br> 2 AF (VYV, BRB) <br> 3 IM (GBB, RSR, SSY) | | |
| | 1997 (8) | 4 AM (YYY, BRR, GBB, RSR) <br> 2 AF (VYV, RBY) <br> 1 IM (SSY) <br> 1 ISU (VBY) | - 1 AF (BRB) (died) <br> + 1 AF (RBY) (immig), 1 ISU (VBY) (wgr) | 0.25 |
| | 1998 (7) | 4 AM (YYY, BRR, RSR, SSY) <br> 2 AF (VYV, RBY) <br> 1 IF (BSY) | -1 AM (GBB), 1 ISU (VBY) (both died) <br> + 1 IF (BSY) (wgr) | 0.143 |
| | 1999 (7) | 4 AM (YYY, BRR, RSR, SSY) <br> 3 AF (VYV, RBY, BSY) | No change | 0 |
| | 2000 (6) | 3 AM (YYY, RSR, SSY) <br> 3 AF (VYV, RBY, BSY) | -1 AM (BRR) (died) | 0 |
| | 2001 (8) | 3 AM (YYY, RSR, SSY) <br> 3 AF (VYV, RBY, BSY) <br> 2 IM (VB, SP) | + 2 IM (VB, SP) (both wgr) | 0.25 |
| | 2002 (9) | 3 AM (YYY, RSR, SSY) <br> 3 AF (VYV, RBY, BSY) <br> 2 IM (VB, SP) <br> 1 ISU (RR) | + 1 ISU (RR) (wgr) | 0.111 |
| | 2003 (7) | 4 AM (YYY, RSR, SSY, VB) <br> 3 AF (VYV, RBY, BSY) | - 1 IM (SP), 1 ISU (RR) (both died) | 0 |

| Group | Year(s) \ (group size) | Composition | − Losses<br>+ Recruits | Proportion comprising recruits |
|---|---|---|---|---|
| | 2004<br>(7) | 4 AM (YYY, RSR, SSY, VB)<br>3 AF (VYV, RBY, BSY) | No change | 0 |
| | 2005<br>(8) | 4 AM (YYY, RSR, SSY, VB)<br>3 AF (VYV, RBY, BSY)<br>1 IF (VY) | + 1 IF (VY) (wgr) | 0.125 |
| | 2006<br>(11) | 3 AM (YYY, SSY, VB)<br>4 AF (VYV, RBY, BSY, VY)<br>4 ISU (U21, U22, U23, U24) | −1 AM (RSR) (died)<br>+ 4 ISU (U21, U22, U23, U24) (all wgr) | 0.364 |
| | 2007<br>(9) | 3 AM (YYY, SSY, VB)<br>4 AF (VYV, RBY, BSY, VY)<br>2 ISU (two of U21-U24) | −2 ISU (two of U21-U24) (fate unknown) | 0 |
| OV | 1996<br>(6) | 2 AM (GGY, YGR)<br>2 AF (RBB, SRB)<br>2 IM (BYG, BSR) | | |
| | 1997<br>(6) | 3 AM (GGY, YGR, BYG)<br>2 AF (RBB, SRB)<br>1 IM (BSR) | No change | 0 |
| | 1998<br>(6) | 4 AM (GGY, YGR, BYG, BSR)<br>2 AF (RBB, SRB) | No change | 0 |
| | 1999<br>(7) | 4 AM (GGY, YGR, BYG, BSR)<br>2 AF (RBB, SRB) | + 1 ISU (GB) (wgr) | 0.143 |
| | 2000<br>(6) | 4 AM (GGY, YGR, BYG, BSR)<br>2 AF (RBB, SRB) | −1 ISU (GB) (died) | 0 |
| | 2001<br>(10) | 4 AM (GGY, YGR, BYG, BSR)<br>2 AF (RBB, SRB)<br>2 IM (PP, YS)<br>2 ISU (SB, BY) | + 2 IM (PP, YS), 2 ISU (SB, SY) (all wgr) | 0.4 |
| | 2002<br>(8) | 4 AM (GGY, YGR, BYG, BSR)<br>1 AF (RBB)<br>3 IM (PP, YS, BB) | −1 AF (SRB), 2 ISU (SB, BY) (all died)<br>+ 1 IM (BB) (wgr) | 0.125 |
| | 2003<br>(9) | 6 AM (GGY, YGR, BYG, BSR, PP, YS)<br>2 AF (RBB, RBG)<br>1 IM (BB) | + 1 AF (RBG) (immig) | 0.111 |
| | 2004<br>(8) | 7 AM (GGY, YGR, BYG, BSR, PP, YS, BB)<br>1 AF (RBG) | −1 AF (RBB) (died) | 0 |
| | 2005<br>(7) | 6 AM (GGY, YGR, BYG, BSR, YS, BB)<br>1 AF (RBG) | −1 AM (PP) (died) | 0 |
| | 2006<br>(9) | 6 AM (GGY, YGR, BYG, BSR, YS, BB)<br>1 AF (RBG)<br>2 ISU (U25, U26) | + 2 ISU (U25, U26) (both wgr) | 0.2 |
| | 2007<br>(6) | 6 AM (GGY, YGR, BYG, BSR, YS, BB)<br>1 AF (RBG)<br>3 ISU (U25, U26, U27) | + 1 ISU (U27) (wgr) | 0.1 |
| SM | 1996-1997<br>(6) | 3 AM (YRY, RBR, BBY)<br>3 AF (BRB, YG, VBV) | | |
| | 1998<br>(3) | 2 AM (YRY, RBR)<br>1 AF (BRB) | −1 AM (BBY), 2 AF (YYG, VBV) (all died) | 0 |
| | 1999<br>(5) | 2 AM (YRY, RBR)<br>1 AF (BRB)<br>1 IF (GY)<br>1 ISU (BP) | + 1 IF (GY), 1 ISU (BP) (both wgr) | 0.4 |
| | 2000<br>(4) | 2 AM (YRY, RBR)<br>2 AF (BRB, GY) | − 1 ISU (BP) (died) | 0 |
| | 2001<br>(6) | 2 AM (YRY, RBR)<br>2 AF (BRB, GY)<br>1 IF (PS)<br>1 ISU (BS) | +1 IF (PS), 1 ISU (BS) (both wgr) | 0.333 |
| | 2002<br>(5) | 2 AM (YRY, RBR)<br>3AF (BRB, GY, PS) | −1 ISU (BS) (died) | 0 |
| | 2003<br>(5) | 1 AM (RBR)<br>2 AF (BRB, GY)<br>1 IM (YR)<br>IF (RR) | −1 AM (YRY), 1 AF (PS) (both died)<br>+ 1 IM (YR), 1 IF (RR) (both wgr) | 0.4 |
| | 2004<br>(6) | 1 AM (RBR)<br>3 AF (BRB, GY, RR)<br>1 IM (YR)<br>1 ISU (BS) | + 1 ISU (BS) (wgr) | 0.167 |
| | 2005<br>(7) | 3 AF (BRB, GY, RR)<br>2 IM (RS, YR)<br>1 IF (RB)<br>I ISU (YB) | −1AM (RBR), 1 ISU (BS) (both died)<br>+ 1 IM (RS), 1 IF (RB), 1 ISU (YB) (all wgr) | 0.429 |

| Group | Year(s) \ (group size) | Composition | - Losses<br>+ Recruits | Proportion comprising recruits |
|---|---|---|---|---|
| | 2006<br>(6) | 1 AM (YR)<br>4 AF (BRB, GY, RR, RB)<br>1 IM (RS) | -1 ISU (YB) (died) | 0 |
| | 2007<br>(5) | 2 AM (YR, RS)<br>3 AF (BRB, GY, RR) | -1 AF (RB) (died) | 0 |
| PG2 | 1996<br>(8) | 4 AM (RRS, SBB, CF, RYY)<br>2 AF (SSR, OL)<br>1 IM (SYS)<br>1 ISU (VBB) | | |
| | 1997<br>(6) | 4 AM (RRS, SBB, CF, RYY)<br>1 AF (OL)<br>1 IM (SYS) | - 1 AF (SSR), 1 ISU (VBB) (both died) | 0 |
| | 1998<br>(3) | 2 AM (SBB, CF)<br>1 AF (U28) | - 2 AM (RRS, RYY), 1 AF (OL) (all died), 1 IM (SYS) (disp)<br>+ 1 AF (U28) (immig) | 0.333 |
| | 1999<br>(5) | 2 AM (SBB, CF)<br>3 AF (YRS, YSS, VVR) | -1 AF (U28) (died)<br>+ 3 AF (YRS, YSS, VVR) (all immig) | 0.6 |
| | 2000<br>(4) | 2 AM (SBB, CF)<br>2 AF (YSS, VVR) | -1 AF (YRS) (died) | 0 |
| | 2001<br>(3) | 1 AM (CF)<br>2 AF (YSS, VVR) | -1 AF (SBB) (died) | 0 |
| | 2002<br>(3) | 1 AM (YP)<br>2 AF (YSS, VVR) | -1 AM (CF) (died)<br>+ 1 AM (YP) (immig) | 0.333 |
| | 2003-2007<br>(3) | 1 AM (YP)<br>2AF (YSS, VVR) | No change | 0 for 2003- 2007 |
| WB | 1996<br>(5) | 2 AM (SRR, YYS)<br>2 AF (GRY, VRB)<br>1 IM (BSS) | | |
| | 1997<br>(5) | 2 AM (SRR, YYS)<br>1 AF (VRB)<br>1 IM (BSS)<br>1 ISU (VBY) | -1 AF (GRY) (died)<br>+ 1 ISU (VBY) (wgr) | 0.2 |
| | 1998<br>(4) | 3 AM (SRR, YYS, BSS)<br>1 AF (VRB) | - 1 ISU (VBY) (died) | 0 |
| | 1999<br>(5) | 3 AM (SRR, YYS, BSS)<br>1 AF (VRB)<br>1 ISU (U30) | + 1 ISU (U30) wgr | 0.2 |
| | 2000<br>(6) | 3 AM (SRR, YYS, BSS)<br>1 AF (VRB)<br>1 IM (YP)<br>1 ISU (GS) | -1 ISU (U30) (died)<br>+ 1 IM (YP), 1 ISU (GS) (both wgr) | 0.333 |
| | 2001<br>(7) | 4 AM (SRR, YYS, BSS, YP)<br>1 AF (VRB)<br>1 IM (U31)<br>1 IF (YG) | -1 ISU (GS) (disp)<br>+ 1 IM (U31), 1 IF (YG) (both wgr) | 0.286 |
| | 2002<br>(6) | 3 AM (SRR, YYS, BSS)<br>1 AF (VRB)<br>1 IM (U31)<br>1 IF (BV) | -1 AM (YP), 1 IF (YG) (both disp)<br>+1 IF (BV) (wgr) | 0.167 |
| | 2003<br>(7) | 3 AM (SRR, YYS, BSS)<br>1 AF (VRB)<br>2 IM (BY, U31)<br>1 ISU (GR) | -1 IF (BV) (disp)<br>+ 1 IM (BY), 1 ISU (GR) (both wgr) | 0.286 |
| | 2004<br>(2) | 1 AF (VRB)<br>1 IM (BY) | -3 AM (SRR, YYS, BSS), 1 IM (U31), 1 ISU (GR) (all died) | 0 |
| | 2005<br>(3) | 1 AF (VRB)<br>1 IM (BY)<br>1 ISU (RV) | + 1 ISU (RV) (wgr) | 0.333 |
| WS | 2003<br>(3) | 2 AM (BPS, BY)<br>1 AF (YY) | | |
| | 2004<br>(3) | 2 AM (BPS, BY)<br>1 AF (YY) | No change | 0 |
| | 2005<br>(3) | 2 AM (BPS, BY)<br>1 AF (RBY) | -1 AF (YY) (died)<br>+ 1 AF (RBY) (immig) | 0.333 |
| | 2006<br>(5) | 2 AM (BPS, BY)<br>1 AF (RBY)<br>1 IM (U32)<br>1 ISU (U33) | + 1 IM (U32), 1 ISU (U33) (both wgr) | 0.4 |
| | 2007<br>(4) | 2 AM (BPS, BY)<br>1 AF (RBY)<br>1 IM (U32) | -1 ISU (U33) (died) | 0 |