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Survival and sex ratio in a mainland population of bellbirds (*Anthornis melanura*)

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Abstract: Both apparent annual survival and population composition were estimated, by age and sex, for bellbirds (*Anthornis melanura*) from a banding study undertaken on a mainland lowland farm at Pleasant Valley, near Geraldine, New Zealand, during the period 1977-97. The model with the fewest parameters showed that apparent survival varied little between sex and years. Although based on only a few recaptures of subadults, apparent survival of adults (0.694 ± 0.042) was slightly greater than that of sub-adults (0.662 ± 0.128). Annual recapture probabilities of adults (0.104 ± 0.024) were also greater than those of sub-adults (0.042 ± 0.029). A comparison of survival and sex ratios between this population of bellbirds and that on the predator-free Poor Knights Islands showed that demographic parameters vary within this species. The mainland population exhibited a lower overall adult survival rate and more even sex ratio than did the island population. Such demographic variation within a species indicate habitat-specific population parameters.

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INTRODUCTION

In New Zealand, the avifauna had been stable in composition, and largely in distribution, for about 10,000 years (Worthy, 1999), until the arrival of humans (Holdaway 1989; McGlone 1989). Subsequent to human arrival, many bird species became extinct, or at the very least their distribution changed markedly. These declines occurred at different times and rates depending on the ecology and life history of each species which made them vulnerable to habitat loss, hunting, predation, and competition for food resources (Holdaway 1989). The distributions and broad habitat associations of extant endemic birds during the period 1999-2004 are now well known (Robertson *et al.* 2007), and for some endemic species a comparison of their distribution estimated for the period 1969-1979 (Bull *et al.* 1985) shows further fragmentation and/or reduction in the area of their occurrence (Robertson *et al.* 2007). However, little information is available that indicates which demographic parameters are influencing such changes in distribution.

Advances in the development of capture-recapture analyses during recent years, especially with respect to survival rates and movement

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probabilities, have enhanced the information that can be determined from banding studies. Mist netting has become an important technique in ornithological capture-mark-recapture studies and it has become the standard means of undertaking several extensive long-term population studies, such as the Constant Effort Sites (CES) scheme organized by the British Trust for Ornithology, the aim of which is to monitor changes in abundance, breeding success and survival rates of a range of common passerine species (Peach *et al.* 1998). Information about survival rates of passerines is critical to our understanding of the factors leading to wide-scale population changes (Peach *et al.* 1999), but few such analyses in natural populations have been reported in New Zealand (Sagar & Scofield 2006).

The bellbird (*Anthornis melanura*) is the more widespread of the 2 honeyeaters (Meliphagidae) that are endemic to New Zealand. They are abundant and widespread in indigenous forests of mainland New Zealand with the exception of Northland, and on most forested offshore islands from the Three Kings (34˚S, 172˚E) in the north, south to the Auckland Islands (51˚S, 166˚E) (Heather & Robertson 1996; Robertson *et al.* 2007).

In this study we present a quantitative analysis of banding data collected over 21 years at one site to estimate adult and sub-adult survival, and population composition, by age and sex. Using these data we compare estimates derived using the same analytical methods from a study of bellbirds on an island free of terrestrial predators to provide an insight into how demographic traits may vary within a species in different habitats and with different predation pressures.

METHODS

Study site

The study was carried out from January 1977 to December 1997 on a lowland farm (44˚05’S, 171˚10’E) at Pleasant Valley, South Island, New Zealand. The lowland farm is situated in a river valley bounded by a river terrace that gives away to rolling hills. Land use in the valley consists of pasture grazed by sheep and cattle. The river terrace had been burned annually until 1947, but not since. Subsequently, it became forested, with the main canopy species being manuka (*Kunzea ericoides*), totara (*Podocarpus totara*), mahoe (*Melicytus ramiflorus*), *Myrsine divaricata*, *Griselinia littoralis* and the introduced sycamore (*Acer pseudoplatanus*). The under-storey comprised mainly *Coprosma* spp and blackberry (*Rubus fruticosus*). Introduced mammals, particularly brushtail possum (*Trichosurus vulpecula*), house mouse (*Mus musculus*), Norway rat (*Rattus norvegicus*), ship rat (*R. rattus*), stoat (*Mustela ermine*), weasel (*M. nivalis*), ferret (*M. furo*), European rabbit (*Oryctolagus cuniculus*), and brown hare (*Lepus europaeus*) are present throughout the farm, including the forested areas. Other terrestrial birds breeding in the forest were silvereye (*Zosterops lateralis*), fantail (*Rhipidura fuliginosa*), grey warbler (*Gerygone igata*), rifleman (*Acanthisitta chloris*), and the introduced blackbird (*Turdus merula*), song thrush (*T. philomelos*), chaffinch (*Fringilla coelebs*), goldfinch (*Carduelis carduelis*), greenfinch (*C. chloris*), redpoll (*Acanthis flammea*), and dunnock (*Prunella modularis*).

Banding

Data were analyzed from a long-term banding study of bellbirds. Netting effort was relatively constant throughout the study. Bellbirds were caught in 12 x 2 m 38 mm mesh mist nets operated from early morning to dusk on at least 3 overcast and calm days in each of summer (December-February), autumn (March-May), and winter (June-August) annually from December 1977 to December 1997, with the exception of the summers of 1992, 1995 and 1996 and winter 1995. At all times 1-2 nets were erected in the garden adjacent to the homestead, usually close to plants that provided food for bellbirds (*e.g.*, nectar from flax (*Phormium tenax*) flowers, nectar or fruit from laurel (*Laurus nobilis*), and fruit from apple (*Malus domestica*) and pear (*Pyrus communis*) trees). The bellbirds did not breed in the garden, but subsequent observations of banded birds showed that they travelled at least 300 m across pasture from breeding territories on the adjacent river terrace. Thus the garden was not included in any bellbird territory and no bellbirds were observed defending any of the food trees as a resource.

Captured bellbirds were aged as sub-adult (birds that had fledged during the previous September to December and had not yet assumed adult plumage or eye colour) or adult (based on eye colour and plumage – see Bartle & Sagar 1987), sexed (on plumage – Bartle & Sagar 1987; Heather & Robertson 1996), measured (flattened, straightened wing chord to nearest 1 mm) and weighed (to nearest 0.5 g), and fitted with a uniquely numbered stainless steel band before release. Sub-adult birds were identified during summer and autumn only because by the end of April all had moulted into full adult plumage and had attained adult eye colour (Bartle & Sagar 1987).

Analysis

An analysis of capture-recapture data was carried out using Cormack-Jolly-Seber models implemented in the computer program MARK 7.1 (White & Burnham 1999). The terms “capture” and “recapture” are used here to denote, respectively, those birds caught and banded for the first time and those birds previously banded and recaptured at the study site.

Table 1. Total numbers of bellbirds captured and recaptured, by age, sex and season, at Pleasant Valley, near Geraldine, South Canterbury, 1977-1997.

Age/Sex		Summer (December-February)	Autumn (March-May)	Winter (June-August)	Total
Adult female	Captured	16	59	3	78
	Recaptured	9	6	6	21
Subadult female	Captured	10	19	0	29
	Recaptured	0	3	0	3
Adult male	Captured	25	61	7	93
	Recaptured	11	11	7	29
Subadult male	Captured	19	19	0	38
	Recaptured	0	2	0	2
Total		90	180	23	293

The notation used and parameters investigated in this analysis follow Lebreton *et al*. (1992):

Φ_i = Probability that a bird alive and in the study area at i is alive at $i + 1$;

p_i = Probability that a bird at risk of capture at i is captured at $i + 1$.

A general model that was fully time-dependent for Φ and p was taken as the starting point and used as the basis for all goodness of fit analyses (*i.e.*, Φ (time) p (time)). Time in this model refers to an encounter in any 1 year (all seasons combined). The recapture p models with the fewest explanatory parameters were identified (following the methodology of Lebreton *et al.* 1992), by examining time-dependent p on both age classes, constant p on both age classes, and time-dependent p in sub-adult birds only. Age and sex structure (*i.e.*, age*sex*time) was introduced into Φ by distinguishing between adult and sub-adults, and between male and female. A 2-age class structure, adult or sub-adult, was selected because for many New Zealand passerines, sub-adult survival is known to be lower than adult survival (Armstrong *et al.* 2002). We then examined the influence of time-dependent Φ on all 4 age/sex classes, constant Φ on all 4 age/sex classes, and time-dependent Φ in sub-adult birds only. The use of the latter model was based on the grounds that sub-adult Φ is lower than adult Φ in passerines, and is more sensitive to annual variation in environmental conditions (Siriwardena *et al*. 1998). Birds often disperse more in their first year than subsequently, and so we also investigated the significance of transience on the population by allocating sub-adult individuals in their first year after capture a separate survival or age probability using the same methodology as Perret *et al.* (2003).

Corrected Akaike's information criterion (AIC_c) in MARK 7.1 (Cooch & White 2001) was used to select the model with the fewest explanatory parameters from a set of candidate models. The logit link function, in program MARK, was used throughout the modelling procedure, with manual checking.

Goodness of fit of the models was evaluated using RELEASE (White & Burnham 1999) and UCARE (Choquet *et al.* 2001). Details of the application of these tests were provided in White & Burnham (1999), Pradel *et al.* (1997) and Chaloupka *et al.* (1999). A small number of dead recoveries were available to allow a comparison of the parsimony of the models using the Burnham Live and Dead model (Burnham 1993) as implemented in program MARK 7.1. The goodness of fit of the global model was then assessed in absolute terms using a parametric bootstrap approach available in program MARK 7.1 using 100 replicates. To deal with the issues of validity of the bootstrapped goodness of fit test when sampling unequal time intervals (Gimenez *et al*. 2005) we created a general model in which each year (including those not sampled) was included in the model, but in which p was set at zero in those years in which there was no mist netting. In addition, both datasets were tested for over-dispersion using the newly implemented median c-hat procedure in program MARK 7.1. Expectation of further life was calculated from $-1/\ln(\Phi)$ (Seber 1982).

RESULTS

Age and sex composition

The age and sex composition of birds caught during each season are summarised in Table 1. Over the 21 years of this study, 238 bellbirds comprising 93 adult males, 78 adult females, 38 sub-adult males and 29 sub-adult females were captured. Of these birds, 21 adult males, 14 adult females, 2 sub-adult males and 3 sub-adult females were recaptured

Table 2. Comparison of top 9 models for factors affecting survival in bellbirds at Pleasant Valley, Geraldine. The factors considered in survival (Φ) and recapture probability (*p*) models were sex and age, with interactions (*). In addition, models that were not specific for sex, age and year (.) were also tested. Models were selected based on Akaikie's information criterion (AIC_c), the lowest AIC_c indicating the most parsimonious model. *K* is the number of parameters in each model; ΔAIC_c is the difference in AIC_c between the current model and the best model. Those models with $\Delta AIC_c > 6$ have negligible support and were not considered further.

Model	AIC_c	ΔAIC_c	AIC_c weights	Model likelihood	K	Deviance
$\Phi_{(age)}\ p_{(age)}$	377.6158	0	0.23264	1	4	258.05304
$\Phi_{(age)}\ p_{(age)}$ with transience in sub-adult *p*	377.7700	0.1542	0.21538	0.9258	5	256.12943
$\Phi_{(.)}\ p_{(sex*age)}$	378.3193	0.7035	0.16365	0.7034	5	256.67872
$\Phi_{(.)}\ p_{(.)}$	378.9446	1.3288	0.11971	0.5146	2	263.48986
$\Phi_{(age)}\ p_{(age)}$ with transience in sub-adult Φ	379.7639	2.1481	0.07948	0.3416	6	256.02944
$\Phi_{(age)}$ *p*(transience in all ages)	379.8004	2.1846	0.07804	0.3355	6	256.0659
$\Phi_{(sex*age)}\ p_{(.)}$	380.5305	2.9147	0.05417	0.2328	5	258.88996
$\Phi_{(sex*age)}\ p_{(sex*age)}$	381.5533	3.9375	0.03248	0.1396	8	253.58188
$\Phi_{(sex)}\ p_{(sex)}$	382.1216	4.5058	0.02445	0.1051	4	262.55887

at least once, with a total of 55 recaptures being used in this analysis (Table 1). Most birds (179) were caught during autumn, with few (23) caught during winter when fruit and nectar were scarce in the farm orchard.

Overall (all seasons, including recaptures), the male bias in the adult (1.19:1) and subadult (1.31:1) populations was not significant (adults χ^2_1 with Yates' correction = 2.18, $P > 0.05$; subadults χ^2_1 with Yates' correction = 0.81, $P > 0.05$).

Survival estimates and recapture probabilities

The bootstrap goodness of fit tests indicated that, for the observed deviance in the full parameter model, the probability of a deviance, as large as or greater than the observed value, was approximately 0.65 for the Pleasant Valley data. Thus, we can assume an adequate goodness of fit or lack of power to reject the model. Logistic regression estimates of median c-hat (1.16) indicated that these models do not suffer from a significant degree of over-dispersion. When the RELEASE goodness of fit tests were run on the full parameter Cormack-Jolly-Seber model (time-dependent Φ and *p*) using UCARE for the dataset, the models passed TEST2, TEST2.Ct (trap dependence statistic). The dataset failed TEST3, but passed TEST3.Sm indicating that transience (the movement of birds out of the area following initial capture, so they were not available for recapture) was not a significant problem. This was also demonstrated by the fact that models that incorporated transience did not give lower AIC_c values than comparable models that did not account for transience. On closer examination it was found that the data failed TEST3.SR, indicating that survival probabilities were cohort-dependent, and indeed this is what the model selection determined (see below).

Model fitting results indicated strong support for the model Φ(age)*p*(age) (Table 2). Model averaging was not used as parameterisation of models with $\Delta AIC_c < 2$ did not have the same interpretation across all models (Posada & Buckley 2004). A model where sex and age were considered (i.e. Φ(age*sex) *P*(age) had a considerably higher AICc, indicating more parameters, which implies that either males and females of the same age had similar survival rates or we have too few recapture data to examine survival by sex, and resulted in us using just one estimate for each age group. Models incorporating annual survival variation among years had little support. Overall adult (sexes grouped) annual survival was 0.694 (± 0.042) while sub-adult (sexes grouped) annual survival rate was 0.662 (± 0.128) (see Table 3). Recapture probabilities did not vary with sex or among years, but did vary between age classes (Table 3). Mean adult (sexes grouped) recapture probability was 0.104 (± 0.024) while mean sub-adult (sexes grouped) recapture probability was considerably lower at 0.042 (± 0.029) (see Table 3).

With an annual adult survival rate of 0.694, an adult bellbird in this mainland population would have, on average, a reproductive life-span of 2.7 years. Similarly, a sub-adult, with a survival rate of 0.662 would have a life-span of 2.4 years, with the oldest birds surviving over 10 years.

DISCUSSION

Our banding study provides new information about the annual survival and sex ratio in a mainland population of bellbirds. In the present study we found no apparent male bias in the adult sex ratio. This contrasts with the situation on the Poor Knights Islands, where a male-biased adult sex ratio was attributed to a higher survival rate of males (Sagar & Scofield 2006). In a review of adult sex ratios in wild birds, Donald (2007) concluded that male-biased adult sex ratios are common and are probably the result of differential mortality between the sexes rather than skewed offspring sex ratios. For bellbirds this conclusion is supported by both this study and the results of Sagar & Scofield (2006). In the present study there were no apparent differences in either adult sex ratio or adult survival (see below), whilst on the Poor Knights Islands, a marked male bias in the adult sex ratio co-occurred with a significantly higher annual survival estimate of adult males (Sagar & Scofield 2006). In contrast, a 12-year longitudinal study of a reintroduced population of stitchbirds (*Notiomystis cincta*) found that changing adult sex ratio had no effect on adult female survival even when males outnumbered females by 3:1 (Ewen *et al.* (2011). As a result, Ewen *et al*. (2011) concluded that conditions under which sex ratio biases negatively affect population growth remain largely unknown and rarely studied.

In this study we found that apparent survival rates of males and females were not significantly different and that survival of adults was marginally higher than that of sub-adults. The absence of a significant difference in survival rate by sex was surprising as sex-dependent survival is common among farmland passerines in the United Kingdom (Siriwardena *et al.* 1998) and the size disparity between male and female bellbirds (Bartle & Sagar 1987) indicates differences in their ecology. However, we have confidence in the results given that 31% of adult males and 29% of adult females were recaptured. In contrast, the survival estimate of subadults is based on the recaptures of only 2 males and 3 females, most likely because younger birds disperse in their first year, and are less likely to be recaptured; in addition they are likely to incur more risk of mortality (Siriwardena *et al*. 1998). Consequently, our estimates of apparent survival of subadult bellbirds in this study should be viewed with caution.

The estimate of apparent survival rate of adults of 0.692 and estimated maximum life span of over 10 years is supported by Spurr *et al.* (2008) who reported the recapture of a bellbird near Christchurch which was likely to be 8+ years old. Our survival estimates appear to be the first for a mainland population of bellbirds. The only other estimate of survival in bellbirds is for the population on predator-free Aorangi Island, Poor Knights Islands (Sagar & Scofield 2006). In the latter study, the model with the fewest explanatory parameters showed that survival varied little with age, but survival of males (adults and sub-adults combined = 0.813 ± 0.027) was significantly greater than in females (adults and sub-adults combined = 0.564 ± 0.039). In contrast, in the present study, conducted in an area of the mainland inhabited by a range of introduced predators the equivalent model with the smallest number of explanatory variables showed that apparent survival did not vary with sex and varied little with age, with survival estimates of 0.694 (± 0.042) for adults (males and females combined). Despite both sampling programmes operating away from breeding sites the differences in habitat composition, predation risk, sampling intensity, and open (mainland) and closed (island) populations make it difficult to assign a cause to the different survival estimates that were found.

Table 3. Survival rate (Φ) and recapture (*P*) estimates of adult and sub-adult bellbirds at Pleasant Valley, Geraldine during 1977-1997 on the basis of the $\Phi_{(age)}\ P_{(age)}$ model.

Label	Estimate	1 SE	95% Confidence limits
Φ Adults	0.694	0.042	0.605-0.771
Φ Sub-adults	0.662	0.128	0.389-0.857
P Adults	0.104	0.024	0.066-0.162
P Sub-adults	0.042	0.029	0.011-0.151

This paper provides insights into how population parameters vary in a native forest-dwelling passerine. Our results indicate that sex ratio and survival in particular vary with habitat and predation risk, and so indicate that both these population parameters are habitat-specific.

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