Pauw, A., and K. Louw. 2012. Urbanization drives a reduction in functional diversity in a guild of nectar-feeding birds. *Ecology and Society* **17**(2): 27.
http://dx.doi.org/10.5751/ES-04758-170227

Research, part of a Special Feature on Urban ecological and social-ecological research in the City of Cape Town

Urbanization Drives a Reduction in Functional Diversity in a Guild of Nectar-feeding Birds

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ABSTRACT. Urbanization is a widespread and rapidly growing threat to biodiversity, therefore we need a predictive understanding of its effects on species and ecosystem processes. In this paper we study the impact of urbanization on a guild of nectar-feeding birds in a biodiversity hotspot at the Cape of Africa. The guild of four bird species provides important ecosystem services by pollinating 320 plant species in the Cape Floral Region. Functional diversity within the guild is related to differences in bill length. The long-billed Malachite Sunbird (*Nectarinia famosa*) plays an irreplaceable role as the exclusive pollinator of plant species with long nectar tubes. We analyzed the composition of the guild in suburban gardens of Cape Town along a gradient of increasing distance from the nearest natural habitat. Urbanization reduces the functional diversity of the nectarivore guild. Malachite Sunbirds did not penetrate more than 1 km into the city, whereas only the short-billed Southern Double-collared Sunbirds (*Cinnyris chalybea*) occurred throughout the urbanization gradient. The lack of data precludes conclusions regarding the detailed responses of Orange-breasted Sunbirds (*Anthobaphes violacea*) and Sugarbirds (*Promerops cafer*), however their absence across the entire gradient is suggestive of high sensitivity. The functional diversity of this guild of pollinators can potentially be restored, but the pros and cons of this conservation action need to be considered.

Key Words: *bird pollination, citizen science, ecosystem services, hummingbird feeders, mobile link organism, mutualism disruption, nectarivore, resilience, urban ecology, urban planning*

INTRODUCTION

A rapidly increasing portion of the Earth’s surface is urbanized. Thus, a vast new habitat is being created and small islands of the original habitat are isolated in it (Radeloff et al. 2005, McKinney 2006, Grimm et al. 2008). Biologists often focus on the small islands of natural vegetation and ask how species diversity varies with fragment size and distance from the nearest large “mainland” of natural habitat (e.g., Bolger et al. 1997, Pauw 2007). In this paper we focus instead on the urban habitat and ask how birds respond to it.

The study is located in the hyper-diverse fynbos vegetation of the Cape Floral Region of South Africa. In it, the largest urban area is the City of Cape Town. Typical of cities in the Developing World, Cape Town is expanding rapidly and engulfing many small conservation areas and the large Table Mountain National Park (Pauw and Johnson 1999, Sinclair-Smith 2009). Our study group is the small guild of specialized nectarivorous birds that occur in the region. We are particularly interested in their response to urbanization because of the important ecological role that they play as pollinators of about 4% of the flora (320 plant species; Rebelo 1987).

Focusing conservation attention on pollinators is justified by the important ecological role that they play. Generalist pollinators, such as birds, are likely to play keystone ecological roles because, as recent network analysis shows, these species form central nodes that hold pollination webs together (Bascompte et al. 2003). Many specialist plant species depend on these generalist animal species for pollination. However, to assess whether these mutualisms matter from an ecological perspective, it is always important to ask where seed set is pollen limited and whether population growth rate is seed limited (Anderson et al. 2011, Pauw and Bond 2011).

As landscapes become increasingly heterogeneous and habitats more fragmented, mobile organisms, especially pollinators and seed dispersers, take on another increasingly important role by acting as links between separated landscape elements (Lundberg and Moberg 2003). By moving across barriers, pollinators maintain gene flow networks that can rescue small isolated plant populations from inbreeding depression.

Additionally, pollinators can contribute to the resilience of ecosystems, i.e., increase the probability that the system will return to its desirable former state following a disturbance (Folke 2006). Fires, which are often anthropogenic, are one example of such disturbances that are becoming increasingly frequent. Nectar-feeding birds could potentially enhance the ability of fynbos vegetation to return to its former desirable state by enhancing seed set in bird-pollinated plants. Especially important are the large, bird-pollinated Proteaceae and Ericaceae shrubs that depend entirely on seeds for regeneration after all the adult plants are fire-killed. These shrubs dominate many fynbos landscapes where they help to retain the soil, improve water quality, suppress alien plants, enhance tourism, provide flowers for the cut-flower industry, and enhance biodiversity (Van Wilgen 1992).

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Despite their ecologically important role, the nectarivore guild in the Cape Floral Region is surprisingly depauperate, essentially consisting of only four bird species. As a result each species performs an important function with limited overlap among guild members. This low level of functional redundancy is likely to be coupled with what might be called a low level of response diversity, meaning that it is likely that all of the species in the functional guild will respond to an environmental change, such as urbanization, in the same way (Elmqvist et al. 2003). As a result, the ecological function, in this case bird-pollination, may be entirely lost. The aim of this paper is to explore response diversity among the members of this guild. We ask: Do the different nectarivorous birds respond differently to the new urban habitat? Do some species live in it and move through it, while others perceive it as an impermeable barrier?

Surprisingly, several studies report that at least some specialized nectarivorous birds can penetrate deep into the interior of cities. In Melbourne, Australia, two species of nectarivorous lorikeets (Psittacidae) have greatly increased in abundance in the urban areas where they feed on planted *Eucalyptus* (Smith and Lill 2008). In Sydney, at least two species of honeyeaters (Meliphagidae) occur in urban areas where they feed on indigenous Proteaceae (French et al. 2005). Ten species of hummingbird (Trochilidae) occur in urban areas of southern Brazil where they feed mainly from exotic, insect-pollinated plants (Mendonça and dos Anjos 2005); while in Mexico City three species of hummingbirds visit *Salvia* species (Arizmendi et al. 2007).

More systematic surveys of birds in urban areas paint a similar picture of tolerance among some nectarivorous birds. Nectarivores were found to be more abundant in developments than in adjacent rural areas in Arizona, USA, presumably because hummingbird feeders and ornamental nectar plants made urbanized areas more attractive than the surrounding arid landscape. In New South Wales, Australia, the nectarivore guild was more likely than the insectivore guild to cross the boundary from natural into urban areas, and was more likely to cross at boundaries with high, rather than low density housing (Hodgson et al. 2007).

Gradient studies provide a detailed and predictive understanding of the ability of birds to penetrate the urban habitat. These studies explicitly test the effect of urbanization by treating “degree of urbanization” as the predictor variable and bird abundance and diversity as the response variables (Chace and Walsh 2006). One such study in California, USA, found that Anna’s Hummingbird (*Calypte anna*) occurred across the entire gradient from conservation area through to central business district, with abundance peaking in the residential area (Blair 1996). In contrast, a study of the bird fauna of remnants of natural vegetation in California found that Costa’s Hummingbird (*Calypte costae*) is sensitive to the fragmentation of its natural habitat by urbanization (Bolger et al. 1997). Together, the studies suggest response diversity among the members of the avian nectarivore guild when faced with urbanization, but in the latter study no surveys were conducted inside the urban matrix.

In this paper, we examine for the first time how African nectarivores respond to urbanization. To do so, we analyze the occurrence of birds in suburban gardens in relation to a gradient of increasing distance from the nearest natural habitat. The results indicate response diversity among the members of the nectarivorous bird guild, but very low permeability of urban areas by at least one functionally irreplaceable pollinator. The interesting challenge of restoring this pollination guild and the ecological services that it provides is discussed.

METHODS

Study area and species

The City of Cape Town has grown from 8000 ha to 38,000 ha since 1950 (Sinclair-Smith 2009). The natural vegetation of the area is a fire-prone shrubland, often dominated by bird-pollinated Proteaceae or Ericaceae. Geophytes, primarily Iridaceae and Amaryllidaceae, provide additional nectar resources for birds. In the South Western Cape, the specialist nectarivorous guild consists of only four bird species: Cape Sugarbird (*Promerops cafer*), Malachite Sunbird (*Nectarinia famosa*), Orange-breasted Sunbird (*Anthobaphes violacea*), and Southern Double-collared Sunbird (*Cinnyris chalybea*). The species are listed in order of declining body size and bill length, a possible indicator of level of dietary specialization. Cape Sugarbirds are closely associated with the Proteaceae; Malachite Sunbirds are the exclusive pollinators of plant species with long tubular flowers mostly in the Iridaceae and Amaryllidaceae; Orange-breasted Sunbirds specialize on the Ericaceae; and Southern Double-collared Sunbirds are generalists (Skead 1967, Geerts and Pauw 2009).

Bird distribution data

Bird occurrence data were collected during 2002 and 2003 by the members of the Cape Bird Club for the Birds in Gardens Project, which was coordinated by the second author (Appendix 1). Participants recorded presence/absence checklists for 46 gardens. Each checklist spanned one day. Between 12 and 381 checklists were available for each of the 46 gardens (median = 139). Presence/absence data were converted to a “reporting rate” by dividing the number of occurrences by the number of checklists available for the particular garden. Our sample of gardens is biased toward the leafy suburbs where birdwatchers live, and this might lead to the underestimation of urbanization effects.

Urbanization gradient

Bird occurrence in gardens was related to “distance from natural vegetation.” This is the same as distance into the city

Table 1. Effect of distance from natural vegetation (natural log of km) on bird reporting rate in suburban gardens analyzed by generalized linear models (error structure = quasi-binomial; link function = logit). Values are on the logit scale. * = factors significant at the p < 0.05 level.

Dependent Variable	Coefficient	Estimate	Std. Error	t-value	Pr(>|t|)
Malachite Sunbird (*Nectarinia famosa*) reporting rate	Intercept	-3.3570	0.4596	-7.303	< 0.0001
	Distance from natural vegetation	-0.8566	0.2213	-3.870	0.0004*
Southern Double-collared Sunbird (*Cinnyris chalybea*) reporting rate	Intercept	-0.5685	0.1924	-2.954	0.00502
	Distance from natural vegetation	-0.3052	0.1501	-2.033	0.04812*
Orange-breasted Sunbird (*Anthobaphes violacea*) reporting rate	Intercept	-4.3433	0.5741	-7.566	< 0.0001
	Distance from natural vegetation	-0.1596	0.3946	-0.404	0.688
Sugarbird (*Promerops cafer*) reporting rate	Intercept	-5.0397	0.5946	-8.476	< 0.0001
	Distance from natural vegetation	-0.4656	0.3060	-1.522	0.135

from the urban edge. In all cases the nearest urban edge is a proclaimed conservation area, i.e., typically various parts of the Table Mountain National Park or the Tygerberg Nature Reserve.

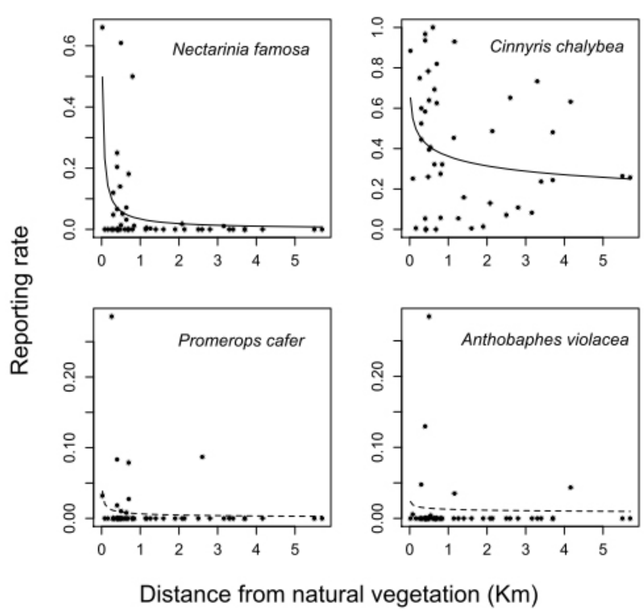
Statistical analyses

The relationship between "reporting rate" and "log (distance from natural vegetation)" was analyzed separately for each of the four bird species in the statistical software R version 2.10, using generalized linear models (GLM) with a logit link function (R Development Core Team 2009). The total number of checklists for a garden was the number of "trials," and the number of checklists that reported the presence of the bird species was the number of "successes." A quasi-binomial error structure was used to account for over-dispersion of the data, which probably resulted from the nonindependence of sample days within each garden. Model prediction were back-transformed from the logit values and plotted.

RESULTS

Malachite Sunbirds and Southern Double-collared Sunbirds responded very differently to the urban habitat: Malachite Sunbirds did not penetrate more than 1 km into the city, whereas Southern Double-collared Sunbirds occurred throughout and showed a gradual decline in reporting rate along the urbanization gradient (Table 1, Fig. 1). The lack of data precludes clear conclusions regarding the detailed response of Orange-breasted Sunbirds and Sugarbirds to the urbanization gradient, however their absence across the entire gradient is suggestive of high sensitivity.

Fig. 1. Four species of nectar-feeding birds show differential responses to increasing urbanization. Each point is one of 46 suburban gardens located at various distances from the nearest natural vegetation. Solid lines are significant model predictions. Dashed lines are predictions from nonsignificant models. Common names are in Table 1.



DISCUSSION

Overall, we detected a diversity of responses to urbanization among the members of the nectarivorous bird guild. With increasing distance from the nearest natural vegetation, guild diversity was reduced from four species to one. Only the generalist Southern Double-collared Sunbird occurs throughout the urbanization gradient. Sugarbirds and Orange-breasted Sunbirds apparently do not penetrate into the city at all, whereas Malachite Sunbirds only occur within 1 km from the nearest natural vegetation.

The strong difference in the response by Malachite Sunbirds and Southern Double-collared Sunbirds to the urbanization gradient (Table 1, Fig. 1) might result from differences in feeding ecology (Evans et al. 2011). Malachite Sunbirds have longer bills than Southern Double-collared Sunbirds (32 vs. 20.5 mm) and are heavier (18 vs. 8 g; Rebelo 1987). As a result, Malachite Sunbirds tend to feed from flowers with longer tubes, and are drawn toward large nectar resources in the landscape (Geerts and Pauw 2009). Southern Double-collared Sunbirds can exploit both short and long-tubed flowers, the latter by puncturing the corolla, and can utilize small nectar resources. It seems likely then that the urban habitat provides sufficient nectar for Southern Double-collared Sunbirds, but not for Malachite Sunbirds. The sudden drop-off in the reporting rate of Malachite Sunbirds at distances greater than 1 km from the nearest natural vegetation suggests that individuals along the perimeter of the city are dependent on resources in nearby natural areas. The contrast sketched here suggests a global analysis of the relationship between nectarivore traits, e.g., bill length and weight, and responses to urbanization. Previous studies on plants (Williams et al. 2009), beetles (Sadler et al. 2006), birds (Carrete and Tella 2011, Evans et al. 2011), and bees (Cane et al. 2006, Ahrné et al. 2009) have been successful in identifying traits that predict responses to urbanization.

The lack of data precludes a detailed understanding of the response of Orange-breasted Sunbirds and Sugarbirds to the urbanization gradient (Fig. 1, Table 1). Ideally, this study should have included surveys in natural habitat. Such surveys, recorded in *The Atlas of Southern African Birds*, indicate that both Sugarbirds and Orange-breasted Sunbirds occur at frequencies similar to those of Malachite Sunbirds and Southern Double-collared Sunbirds in natural habitat adjoining the urban areas (Harrison et al. 1997). Hence, we interpret the consistently low reporting rates for the urban area as a preliminarily indication of very high sensitivity to urbanization. Sugarbirds (37 g) are twice as heavy as Malachite Sunbirds and their consequentially larger nectar requirements could explain their absence from urban areas. The same is not true for Orange-breasted Sunbirds (10 g, bill length 21 mm), and their absence from urban areas begs explanation. Our earlier work shows that Orange-breasted Sunbirds are sensitive to road traffic (Geerts and Pauw 2011), while other studies suggest that fear of humans and vehicles is an important trait that predicts bird responses to urbanization (Carrete and Tella 2011).

How is the observed reduction in bird diversity due to urbanization likely to affect pollination? Lesser Double-collared Sunbirds might to an extent be able to replace the lost services provided by Orange-breasted Sunbirds, which have similar bill lengths, and can play a role in pollinating certain Proteaceae species in the absence of Sugarbirds. These plant species that are pollinated by more than one bird species will benefit from the functional redundancy in the guild and the diversity of responses among guild members in the face of disturbance. However, there is limited functional redundancy in the guild. In particular, the demonstrated sensitivity of Malachite Sunbirds to urbanization is of concern because of the functionally irreplaceable role that this species plays as the exclusive pollinator of plant species with floral tubes in excess of 35 mm (Geerts and Pauw 2009). The endangered *Brunsvigia litoralis* serves as an example. Populations that occur in small fragmented populations, which lack Malachite Sunbirds, suffer reduced seeds set because of severe pollen limitation and experience high rates of nectar robbing by short-billed sunbirds, which pierce holes through the side of the flower to access the nectar. Only Malachite Sunbirds with their longer bills visit the flowers legitimately and transfer pollen (Geerts and Pauw 2012). The loss of this bird species clearly precipitates a loss in functional diversity (Lindberg and Olesen 2001, Petchey and Gaston 2006).

The questions to answer now are: Do we want to restore the nectarivorous bird guild in cities, and how? The restoration of pollination in cities will help to repair broken mutualism and rescue plant populations in urban conservation areas (Pauw and Hawkins 2010, Anderson et al. 2011, Pauw and Bond 2011). For example, Malachite Sunbirds historically occurred at Rondevlei Nature Reserve located inside the city, but are currently absent with implications for long-tubed plant species such as *Brunsvigia orientalis* that occur there (Pauw 2004). Although the nectarivore guild is still intact in the Table Mountain National Park, this extensive conservation area is entirely cut off from other natural areas by the interposition of the City of Cape Town. The opportunity for the creation of continuous green corridors to link these islands no longer exists, but it is possible to make the urban matrix more permeable to nectarivores in an attempt to restore metapopulation dynamics (Colding 2007, Lundberg et al. 2008, Tremblay and St. Clair 2011). The dynamics of local emigration and immigration are likely to be particularly important in fire-prone vegetation, such as fynbos, where nectar availability fluctuates on a 6 to 20 year fire cycle (Pauw 2004, Geerts et al. 2012).

If the distribution of the nectarivorous birds is limited by nectar availability, then restoration is certainly possible by (1) installing bird-feeders in the city, and (2) planting appropriate nectar plants. Potentially, both approaches could be implemented through the schools network and linked to the school curriculum, but the practicalities will have to be thrashed out during workshop sessions. Bird feeders are easy to construct from recycled materials, can be filled with a sugar in water solution, and can be designed to be accessible only by long-billed species. The latter is a physics and chemistry lesson in itself with scope for learning about air-pressure, solutions, and concentrations. However, nectar feeders need to be serviced regularly, so have limited utility for long-term restoration.

The planting of nectar plants in school gardens is likely to have a longer term impact and will bring many additional advantages such as noise pollution reduction and psychological health and well-being (Armstrong 2000, Goddard et al. 2010, Fontana et al. 2011, Lerman and Warren 2011). Schools can be selected to form a series of stepping-stones linking important conservation areas to the nearest natural vegetation (Colding 2007, Tremblay and St. Clair 2011). Plant species will have to be selected based on flowering phenology to provide a yearlong supply of nectar. Learners can easily identify the small number of nectar-feeding birds and report observations via a web-linked cell phone application or electronic social networks, e.g., Twitter.com, MXit.com. Data can be uploaded onto databases such as the citizen science driven Southern African Bird Atlas Project (http://mybirdpatch.adu.org.za), from where the restoration attempt can be monitored.

A project such as this will help to build a meaningful link between urban conservation areas and the surrounding communities, and will be a good test case for conservation action beyond reserve boundaries. Birds can serve as flagships for a broader pollinator restoration project, and pollinator gardens can provide forage for other important pollinators such as bees, which are also impacted by urbanization (Cane et al. 2006, Pauw 2007, Ahrné et al. 2009).

In deciding whether or not to restore the nectar-feeding bird guild, possible negative ecological consequences of restoration should be considered. The first concern is contamination of wild plant populations by genes from horticultural varieties when birds move pollen between urban and natural areas. Horticultural varieties are selected for traits, such as prolonged flowering, that are likely to be maladaptive in a natural setting. The problem of contamination can potentially be overcome if seed is harvested from local seed sources. Second, feeders and garden plants might attract birds away from wild plant populations (Arizmendi et al. 2007), although studies of hummingbirds suggest that birds prefer to visit flowers rather than hummingbird feeders (Inouye et al. 1991, McCaffrey and Wethington 2008). Last, feeders might facilitate the spread of disease among birds, although there is little evidence for this (Saidenberg et al. 2007).

Responses to this article can be read online at:
http://www.ecologyandsociety.org/vol17/iss2/art27/responses/

Acknowledgments:

This paper is a product of the Urban Ecology CityLab which is part of the CityLab programme of the African Centre for Cities at the University of Cape Town. The African Centre for Cities' CityLab programme is funded through the Mistra Urban Futures network (which is funded by Mistra the Foundation for Strategic Environmental Research and the Swedish International Development Cooperation Agency), the Provincial Government of the Western Cape (Department of Human Settlements), and the City of Cape Town. We would like to thank all the citizens who participated in the Birds in Gardens Project, Jan Bengtsson, Carl Folke and one anonymous reviewer for useful input.

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Appendix 1.
Number of days on which nectar feeding birds were observed in urban gardens located at various distances from the nearest natural vegetation.

Surname	**Name**	**Suburb**	***Promerops_cafer***	***Nectarinia_famosa***	***Anthobaphes_violacea***	***Cinnyris_chalybea***	**Total_days**	**Km**
New	Judy	Paarl	8	165	0	221	250	0.02
Russell	GM	Fresnaye	0	0	2	89	354	0.08
Hill_H	Candace	Lakeside	0	0	0	1	164	0.16
Herman	Brian	Lakeside	16	0	0	42	56	0.26
Johnson	Jo	FishHoek	0	3	0	15	25	0.3
McAdam	Anne	FishHoek	0	1	1	11	21	0.3
Gordon	Lynne	Noordhoek	0	0	0	12	27	0.3
Dallas	Evan	Bloubergstrand	0	0	0	6	113	0.4
Berg	Brigitte	Constantia	2	22	14	101	108	0.4
Oosthuizen	Edith	Somerset	1	3	0	7	12	0.4
Morris	SA	Tokai	0	6	0	88	91	0.4
WynneDyke	Ken_Vygeboom	Durbanville	0	0	0	0	111	0.42
Nel	Theo	Milnerton	0	0	0	0	61	0.42
Metcalf	Marilyn	Kommetjie	0	22	0	123	157	0.48
Vogel	X	Welgemoed	0	0	0	50	192	0.48
Hobbs	Jo	Brackenfell	0	2	0	58	147	0.5
Rebelo	A	Durbanville	2	120	56	126	197	0.5
DeVilliers	M_Dbnville	Durbanville	0	13	1	103	254	0.54
Durrant	Rose	Constantia	0	0	0	36	36	0.6
Moll_P	Mike	Paarl	0	2	0	9	28	0.64
Weiss	Yvonne	Paarl	3	12	0	264	381	0.64
WynneDyke	Ken_Sonstraal	Durbanville	0	0	0	0	215	0.68
Ellis	Robert	Durbanville	20	46	0	159	254	0.7
Copeland	Paarl	Paarl	5	0	0	150	183	0.7
Maciver	Margaret	Milnerton	0	26	0	3	52	0.8
Ross	Virginia	Newlands	0	0	0	36	131	0.8
Wordon	Daphne	Durbanville	0	2	0	53	165	0.84
Viljoen	Maureen	Constantia	0	0	0	96	212	1.14
Louw	Kirsten	Constantia	0	1	7	186	200	1.16
WynneDyke	Ken_Hebron	Durbanville	0	1	0	18	330	1.26
Booth	Joan	Constantia	0	0	0	13	82	1.4
Barnes_H	Dick	Rondebosch	0	0	0	1	205	1.6
Burger	Lou	Rondebosch	0	0	0	1	74	1.9
Lockhart	Pat	Constantia	0	3	0	22	169	2.08
VanderVliet	Virginia	Rondebosch	0	0	0	18	37	2.14
Beighton	Peter	Rondebosch	0	0	0	17	238	2.5
Nupen	Peter	Parow	2	0	0	15	23	2.6
Jones	Fiona	Claremont	0	0	0	12	111	2.8
Ledgard	Sylvia	Edgemead	0	4	0	31	375	3.16
Crosswell	Judith	Kenilworth	0	0	0	22	30	3.3
Koeslag2	Ann	Plumstead	0	0	0	31	131	3.4
Adam	Sally	Plumstead	0	0	0	51	209	3.7
Joubert	Audrey	Wynberg	0	0	0	26	54	3.7
Eva	Jean	Kenilworth	0	0	13	189	299	4.16
Kerr	Libby	Parow	0	0	0	24	91	5.5
Anderson	Brenda	Pinelands	0	0	0	95	371	5.7