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Fall 2010

Landscape Factors Impacting Survival of Sympatric Red-Necked Wallabies (Macropus Rufogriseus) and Swamp Wallabies (Wallabia Bicolor) in Urbanized Areas

Karen Zusi *SIT Study Abroad*

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Landscape factors impacting survival of sympatric red-necked wallabies (*Macropus rufogriseus***) and swamp wallabies (***Wallabia bicolor***) in urbanized areas**

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Abstract

 Urbanization and infrastructure build-up often includes many processes that can damage the natural environment in surrounding areas. Road, powerline, and dam construction, as well as mining, drilling, and overall land-clearing, have severe impacts that resonate through the adjacent wildlife communities. Some species, however, are able to persist in the fringes of urban environments; the swamp wallaby, *Wallabia bicolor*, is one such example in Australia. A different species of macropod, the red-necked wallaby (*Macropus rufogriseus*), is similar to the swamp wallaby in many ways but has failed to persist in the outskirts of urban areas. This study aimed to quantitatively differentiate the two species' land and habitat use preferences at a landscape scale and examine how the swamp wallaby has survived close to urban areas while the red-necked wallaby has seemingly vanished in the areas surrounding Sydney. The swamp wallaby was demonstrated to be a generalist selector of habitat type, elevation, and slope, while the red-necked wallaby appeared to prefer open and flat areas; additionally, the swamp wallaby was attracted to urban environments while the red-necked wallaby apparently avoided them. This suite of traits suggests that the red-necked wallaby may have been brought into direct competition with humans when the Sydney area was colonized and been pushed into the forest interior habitats, while the swamp wallaby was able to take advantage of otherwise unsuitable area that was left as remnant vegetation. These results have implications for urban development strategies that must not overlook the specialized species, nor overstress those that appear to be able to persist.

Table of Contents

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1. Introduction

1.1 Scale of human influence

Human impacts on the landscape have increased dramatically with the advent of new technologies spurring land-use and the continued buildup of global infrastructure. Although landuse practices can vary widely, their main purpose is generally to increase the acquisition of natural resources for human consumption, and that rate of human consumption continues to grow as the population expands. However, research into human land use has begun to reveal many of its adverse side effects on the environment (Foley et al. 2005). This influence is exaggerated in many areas that also house high levels of natural biodiversity, a small proportion of land where over one billion humans are estimated to live, including Australia (Cincotta et al. 2000). Urban development has an even more widespread impact. Within Australia alone, 82% of the population resides in urban areas that must continue to grow in order to support such large numbers (Sutton et al. 2010).

1.2 Urban development impacts on the environment

Urban development impacts wildlife in a myriad of ways, many of which are negative. Infrastructure has been linked to major biodiversity losses (reviewed in Benitez-Lopez et al. 2010). Roads, railways, powerlines, dams, mines, drilling, and the land-clearing necessary for construction and maintenance of these technologies all have measurable and degrading effects on the environment.

Habitat loss and fragmentation are major problems for many organisms when human development encroaches upon their ecosystems. Population isolation has been demonstrated via genetic analysis for a number of different species (bank voles, Gerlach and Musolf 2000;,

freshwater turtles, Patrick and Gibbs 2010); this isolation occurs as a result of specialized species not being able or willing to cross open areas, or of otherwise mobile animals attempting to cross a cleared area and being injured or killed. The loss of access to suitable foraging grounds and shrinkage of home ranges are other additive effects of fragmentation that also damage species integrity, particularly that of those species which require pristine interior habitats to survive.

 Development also brings many species into close contact with other human pressures, at least initially. Animals such as kangaroos and dingoes are more vulnerable to being hunted and shot by farmers, regardless of legality, and some species may even be drawn to the urban fringe due to increased food supplies and the ease of moving over open areas (e.g. Coelho et al. 2008). Domestic dogs and cats that frequent the human-populated urban environments can become predators of smaller native wildlife, while many non-native plant species grown in landscaped gardens can quickly disperse to new areas using human-constructed corridors (Hansen and Clevenger 2005).

 Land-clearing and paving lead to increases in pollution (chemical, noise, and light) and erosion as other edge effects, as well. Many species avoid roadside areas in response to the altered microclimate (Carr et al. 2002). Noise pollution has had marked effects on birds, primates, and frogs and may affect their communication structures and survivability by compromising predator avoidance strategies (Parris and Schneider 2009, Parris et al. 2009, Barber et al. 2010). Additionally, the presence of roads and related structures has measurable effects on the integrity of stream and river systems through increased sedimentation or redirection of water flows (reviewed in Coffin 2007).

 In the midst of these largely indirect effects on wildlife populations, urban development also impacts native fauna in a direct and deadly manner: vehicle collisions and roadkillings.

6

Hundreds of different species are killed globally by humans in cars, including turtles, deer, elk, grizzly bears, and amphibians (Bellis and Graves 1971, Hels and Buchwald 2001, Gibbs and Shriver 2002, Beaudry et al. 2008, Frair et al. 2008, Roever et al. 2008). Within Australia, numerous studies have investigated the details of collisions with the large marsupial macropods and wombats, along with smaller mammals, and particularly Tasmanian fauna, of which roadkill rates are reported to be the highest in the country (Coulson 1989, Hobday and Minstrell 2008, Roger and Ramp 2009). Fahrig and Rytwinski (2009) identified four suites of traits that predicted negative responses to the road environment, including species that are attracted to road environments and cannot avoid vehicle collisions, and species with large movement ranges or dispersal patterns that come into contact with roads at high frequencies. When roads bisect migration routes and home ranges of native wildlife, these harmful interactions are inevitable.

1.3 Road-effect zone and the landscape

Most, if not all, results of urbanization impacting the environment can be traced back to road development. The ecological effects of road construction and repeated road usage are not limited to the directly-adjacent roadside, but can extend many meters into the surrounding bushland (Forman and Deblinger 2000). Forman and Deblinger found that this "road effect zone," combining the previously-discussed effects on habitat loss and habitat quality, extended approximately 600 meters on average into surrounding wilderness areas. However, this numerical average does not take into account the fact that often the effect zone is asymmetric in shape and depends largely on the urban factor and organisms being considered. A metastudy by Benitez-Lopez et al. (2010) additionally revealed that mammal and bird populations can be influenced by roads and urbanization over distances up to five kilometers from the edge of the infrastructure system.

The sheer size of this zone and the variation in its shape, in addition to the variation of its effect on organisms, calls for a holistic ecological approach to studying it. Urban managers and developers need to be able to separate the influence of localized site variables in the land (vegetation cover, abundance of different plant species) and landscape-scale variables (cleared areas, built structures, or roads) in order to fully understand its impact on the flora and fauna of the area (Garden et al. 2010). These road impacts can combine with other human-induced disturbances and potentially seal the fate of species living in a matrix of agriculture, urbanization, and remnant bush.

1.4 Why do some species persist?

 The urbanization and explosion of human development has not spelled certain death for all of the world's other species. Behavioral landscape ecology can be a useful tool in predicting how organisms will react to novel human influence with regard to their movements and dispersal, their habitat selection, and their reproductive success (Knowlton and Graham 2010). It is obvious that some species have been able to adapt to urbanization while others have not; what is less obvious is the differences that can account for this adaptability. Some past studies have indicated that species "resistant" to human modifications of native habitat tend to survive based on the breadth of their dietary and habitat needs (Swihart et al. 2003, Bonier et al. 2007). In other words, generalists that can take advantage of shrinking resource amounts have a higher likelihood of withstanding urbanization effects. More flexibility seems to equal more survivability in a human-dominated landscape.

1.5 Macropods and the urban environment

Southwell et al. (1999) report that macropod communities are most diverse in eastern Australia, with the region along the New South Wales and Queensland border supporting nine different species. Eastern Australia also supports the greatest concentration of human populations and the most intense land-use processes (Southwell et al. 1999, Sutton et al. 2010). This junction of native wildlife and human influence has created problems for some species. Notably, the rednecked wallaby (*Macropus rufogriseus*), whose range extended southeast into the Sydney area prior to European colonization, has declined in these areas and is no longer found near the coast (Flannery 2004). However, the swamp wallaby (*Wallabia bicolor*) also thrived in this area prior to European colonization and is still found on the fringes of the urban environment today. Furthermore, this species is often one of the last large- or medium-sized marsupials to survive in such close proximities to humans where other species vanish (Ben-Ami 2005).

The red-necked and swamp wallaby are of similar size and have often been grouped together in studies of macropod behavioral ecology (e.g. Southwell et al. 1999). Unfortunately, the disparity in their apparent survivability rates with regard to urbanization indicates that this approach glosses over other important traits that are not so similar. Past researchers have investigated their habitat use and dietary preferences on small scales, but this study aimed to compare the two species at a landscape-use scale and quantitatively determine what traits or preferences have allowed the swamp wallaby to persist on the outskirts of urbanized areas, complete with all of their anthropogenic disturbances, where red-necked wallabies have failed.

2. Methods

2.1 Study organisms

 The red-necked wallaby is a medium-sized wallaby weighing 15-20 kg on average. It is primarily a grazer, with 84% of its diet typically made up of grass and only 16% made up of woody vegetation (Jarman and Phillips 1989, Sprent and McArthur 2002). It is a solitary animal with home range sizes typically around 15 ha (Johnson 1987), although large feeding aggregations may appear at night in areas with high levels of edible and nutritious vegetation (Johnson 1989). Red-necked wallabies also breed continuously throughout the year, although a partially seasonal pattern has been demonstrated by Higginbottom and Johnson (2000) that noted a higher frequency of joeys emerging from the pouch in the spring.

 The swamp wallaby is similar in size to the red-necked wallaby (measuring at 10-25 kg). However, this species is primarily a browser, with 43% of its diet made up of woody vegetation (Jarman and Phillips 1989, Osawa 1990). Only 14% of its diet consists of grass, with the remaining 43% including a mixture of ferns and fungi. This species is far more cryptic than the red-necked wallaby and does not aggregate in large groups even when feeding; instead, it is mainly a solitary and non-territorial animal (Croft 1989). Home range size is estimated at 15-40 ha (Troy and Coulson 1993).

2.2 Study areas

 This study was undertaken at two different locations in the Blue Mountains region west of Sydney. Locations were chosen based on New South Wales government atlas data of rednecked (**Figure 1**) and swamp wallaby (**Figure 2**) sightings from the Department of Environment, Climate Change and Water.

10

Figure 1. Atlas data of macropod sightings within the Newnes and Lithgow area of the Blue Mountains region. Red dots are red-necked wallaby sightings, blue are Eastern grey kangaroo, dark green are swamp wallaby, pink are common wallaroo, and light green are clusters of sample sites from this study. The area is dominated by red-necked wallaby and Eastern grey kangaroo points.

Figure 2. Atlas data of macropod sightings within the Katoomba area of the Blue Mountains region. Red dots are red-necked wallaby sightings, blue are Eastern grey kangaroo, dark green are swamp wallaby, pink are common wallaroo, and light green are clusters of sample sites from this study. The area is dominated by swamp wallaby points.

 Lithgow and the Newnes State Forest area were the main study sites for red-necked wallabies based on previous records of their distribution. The Newnes State Forest is located at the northwestern end of the Blue Mountains, just north of the town of Lithgow, and lies mainly on a plateau at an elevation of 950 m.

Katoomba and surrounding areas (Wentworth Falls and Lawson) were the main study sites for the swamp wallaby analysis. Katoomba is a small mountain town of 7,600 people approximately 40 km southeast of Lithgow. The town is situated at 1,000 m above sea level.

2.3 Sampling methods

Fieldwork was conducted in three sets, all during November 2010; November 3^{rd} - 7^{th} , 9^{th} -12^{th} , and 16^{th} - 19^{th} . Sampling took place across a three-tiered scale. Within each of the two overall study areas, ten smaller sites were selected for a range of landscape variables (see section 2.5), and within each of these ten sites, between five and ten plots were set up and searched for signs of macropods. Each plot was 5x5 m and laid out using two 10 m long ropes in a square, covering an overall area of 25 m^2 .

Measured signs of macropod activity included faecal pellets, tracks, and direct observations, all of which were recorded, although faecal pellets were the only dependent variable used in data analysis. Track and observational notes were used to confirm species identity in each site if applicable. Each plot was searched for a minimum of ten minutes and all pellets were collected. Many macropods, including swamp and red-necked wallabies, often leave multiple pellets in one group at a time, so pellets were kept in these groups after collection and the total number of pellet groups was the value used during analysis as a measure of frequency of use (Johnson and Jarman 1987).

2.4 Pellet identification

Between November $22nd$ and $23rd$, each collected group of pellets was tested for species identification. Pellets were identified as either swamp wallaby, red-necked wallaby, or "other" based on overall size, shape, and content. At least one pellet from each group was cut open and the contents examined for proportion of grass to woody vegetation, which was then used to differentiate between the three species using dietary percentages from Jarman and Phillips (1989). When conflicting results emerged between size, shape, or content, identification was based on a match to at least two of the three.

 Red-necked wallaby pellets were on average smaller than the swamp wallaby pellets, with a higher percentage of grass compared to woody vegetation. They were also more cylindrical with a point at one end. Swamp wallaby pellets were larger, often a darker color, and more rounded, with a high percentage of woody vegetation and significantly less grass. Pellets classified as "other" were typically square in shape and lacked any woody vegetation, likely either Eastern grey kangaroo, *Macropus giganteus*, or common wallaroo, *Macropus robustus* (Triggs 1997).

2.5 Correlation with landscape variables

Each plot's latitude and longitude were recorded in the field and entered into ArcGIS as a sample point. The following landscape values were then determined for each point: elevation (m), slope (%), distance from permanent natural water sources excluding perennial lakes and streams (m), average annual rainfall in the area (mm), Enhanced Vegetation Index (EVI) mean, number of years since the last bushfire, distance into protected habitat including national parks and state forests (m), distance from protected habitat for points that fell outside the borders of these areas (m), distance from major roads (m), and distance from heavy urbanization (m). This mixture of topographical, biotic, and human-influenced landscape factors yielded a comprehensive picture of the ecological processes at work in each area.

 The values for each of these variables were correlated with the number of pellet groups for red-necked wallabies in Lithgow and Newnes and for swamp wallabies in Katoomba using the software program JMP 9. Both linear and nonlinear patterns were looked for, although nonlinear patterns were only included in the analysis with up to two degrees of freedom. Once each species was investigated individually for significant correlations, they were compared using

13

a linear analysis of covariance (ANCOVA) to determine if the patterns they exhibited were significantly different from each other.

 Additional analysis was done on habitat type and land management status (protected in the form of state forests or national parks versus not protected). Each point was defined as protected or not protected, as well as classified into a particular habitat type based on data obtained through ArcGIS maps, and the pellet densities in each category were averaged and analyzed for variance with Student's t test.

3. Results

3.1 Topographical variables

 Red-necked wallabies displayed a significant linear trend in their distribution with increasing elevation (**Figure 3**). Between 950 m and 1200 m, average pellet group numbers increased from 0 to 3. Swamp wallabies did not display any significant distribution trends with regard to elevation differences, either linearly or nonlinearly. Between 500m and 950m, pellet group averages per sample point remained stable between 0 and 2. When compared, the two species' responses to elevation did not differ significantly, although the base numbers for the comparison were skewed due to the overall elevations of each study area (the lowest sample of red-necked wallaby density was taken 450 meters above the lowest sample of swamp wallaby density).

Figure 3. Average numbers of red-necked wallaby (RNW) and swamp wallaby (SW) pellet groups across an elevation gradient. RNW trend was significant (P = 0.0083, F_{1,61} = 17.1892), but SW was not (P = 0.1544, F_{1,78} = 2.0685). ANCOVA did not reveal a significant relationship (P = 0.0938, $F_{1,139} = 2.8470$).

Red-necked wallabies displayed a significant inverse linear relationship with slope

percentage (**Figure 4**). As the terrain grew steeper and the measured slope percentage increased

to 0.9, the average number of pellet groups decreased to zero. Swamp wallabies did not display a significant pattern with relation to slope. The average number of pellet groups remained relatively constant with slope percentages ranging from 0.0 to 0.9. When compared with each other, the red-necked wallaby and swamp wallaby patterns did not differ significantly.

Figure 4. Average numbers of red-necked wallaby (RNW) and swamp wallaby (SW) pellet groups across a slope percentage gradient. RNW trend was significant (P = 0.0053, $F_{1,61}$ = 8.3547), but SW was not (P = 0.3663, F $_{1,78}$ = 0.8357). ANCOVA did not reveal a significant relationship (P = 0.0829 , F_{1,139} = 3.0510).

Red-necked wallabies displayed a linear trend in their distribution with relation to permanent natural water sources in the landscape such as streams and lakes (not perennial streams) (**Figure 5**). As distance from these water sources increased from 0m to 3000m, the average number of pellet groups in each plot increased from 0 to 3, with values ranging as high as 9 at 2500m. Swamp wallabies did not display a significant trend with relation to water sources. The average number of pellets remained relatively constant at values from 1 to 2 pellet groups per sample point over distances ranging from 0m to 2000m from water sources. When compared, however, no significant difference was found between species.

Figure 5. Average numbers of red-necked wallaby (RNW) and swamp wallaby (SW) pellet groups correlated with distance from permanent natural water sources. RNW trend was significant (P = 0.0134, $F_{1,61}$ = 6.4880), but SW was not (P = 0.5835, $F_{1,78}$ = 0.3031). ANCOVA did not reveal a significant relationship ($P = 0.0904$, $F_{1,139} = 2.9079$).

3.2 Biotic and climactic variables

Red-necked wallabies displayed a significant linear trend in distribution versus average annual rainfall amounts (**Figure 6**). As the average amount of rainfall per year went up from 900mm to 1100mm, the pellet group averages also went up at each site from 0 to 3. Swamp wallabies did not display a similar trend; instead, their pellet group counts followed a significant nonlinear pattern, peaking at an average annual rainfall of 1300mm and decreasing with both more and less rain. When both species were compared linearly, no significant difference was found between them.

Figure 6. Average numbers of red-necked wallaby (RNW) and swamp wallaby (SW) pellet groups across a rainfall gradient. RNW trend was significant (P = 0.0362, F_{1,61} = 4.5889), as was SW trend (P = 0.0128, F_{2,77} = 4.6154). ANCOVA did not reveal a significant relationship (P = 0.4287, $F_{1,139} = 0.6300$).

Using the Enhanced Vegetation Index to estimate greenness and therefore amount of vegetation, no relation was found between either the distribution of red-necked and swamp wallabies individually or when compared to each other (**Figure 7**).

Figure 7. Average numbers of red-necked wallaby (RNW) and swamp wallaby (SW) pellet groups across the Enhanced Vegetation Index gradient. RNW trend was not significant (P = 0.0895, $F_{1,61} = 2.9777$), nor was SW trend (P = 0.5656, $F_{1,78} = 0.3329$). ANCOVA did not reveal a significant relationship ($P = 0.3760$, $F_{1,139} = 0.7886$).

Red-necked wallabies displayed an increasing linear trend in relation to the number of years since the sample points were last burned (**Figure 8**). Each site was burned either 4, 13, or 67+ years ago, and the average number of pellet groups increased along this spectrum. Swamp wallabies did not display a notable trend with relation to the number of years since the last fire. Each site was burned either 8, 9, 17, 30, or 67+ years ago, but the concentration of pellet groups on average did not vary significantly between these values. When compared, the two species displayed significantly different responses to recently-burned areas. Red-necked wallaby pellet groups were in greater average concentrations in areas that had not been burned recently, while swamp wallaby pellet group averages decreased more sharply as the years since the last fire increased.

Figure 8. Average numbers of red-necked wallaby (RNW) and swamp wallaby (SW) pellet groups across a historical fire gradient. RNW trend was barely significant (P = 0.0526, $F_{1,61} = 3.9068$), but SW trend was not (P = 0.0777, $F_{1,78} = 3.1967$). However, ANCOVA did reveal a significant relationship ($P = 0.0109$, $F_{1,139} = 4.6518$).

3.3 Human-influenced variables

Red-necked wallabies displayed a nonlinear distribution pattern with increasing distance into protected areas (away from the border) (**Figure 9**). If a plot fell outside the border of a national park or state forest, it was measured as a zero. The average number of pellet groups peaked at 4 at a distance of 2750m into the parks and state forests, and decreased with both longer and shorter distances. Swamp wallabies displayed a strictly linear significant distribution trend in relation to distance into protected habitat. As the distance from the border increased from 0 up to 5000m, the average number of pellet groups in each sampling point decreased from 2.5 to 0. When compared, the two species' patterns differed significantly from each other. The red-necked wallaby pellet numbers increased on average with increasing distance into the state forests and national parks, and swamp wallaby pellet numbers decreased.

Figure 9. Average numbers of red-necked wallaby (RNW) and swamp wallaby (SW) pellet groups between distance into protected habitat. RNW trend was significant (P = 0.0038, F_{2,60} = 6.1319), as was SW trend (P < 0.0001, F_{1,78} = 17.420). ANCOVA did reveal a significant relationship (P < 0.0001, $F_{1,139} = 17.1892$).

Red-necked wallabies displayed a linear trend in their distribution outside of state forests and parks (**Figure 10**). As distance from the border of protected land increased from 0m to 3000m, the number of pellet groups decreased significantly from an average of 3 to 0. Swamp wallabies displayed an opposite distribution pattern. As distance from protected habitat increased from 0m up to 400m, their average pellet group count increased significantly in a linear pattern from 1 to 8. When compared, the two species differed significantly in their responses to protected habitat areas; red-necked wallaby numbers decreased on average the farther away from protected habitat samples were taken, and swamp wallabies increased with increasing distances from protected areas.

Figure 10. Average numbers of red-necked wallaby (RNW) and swamp wallaby (SW) pellet groups between distance from protected habitat. RNW trend was significant (P = 0.0015, $F_{1,61} = 11.0337$), as was SW trend (P < 0.0001, $F_{1,78} = 45.8937$). ANCOVA did reveal a significant relationship ($P < 0.0001$, $F_{1,139} = 47.1718$).

Red-necked wallabies displayed a nonlinear trend in their distribution with relation to major roads, with the highest average number of pellets occurring at about 3500m from the nearest major road (**Figure 11**). Distances less than 3500m and greater than 3500m saw fewer pellet groups. Swamp wallabies likewise displayed a nonlinear trend in distribution; however, their highest average number of pellets occurred at 1000m from the road, with pellet group numbers sharply decreasing at longer and shorter distances. When compared, the two species on average had significantly different linear responses to roads; red-necked wallabies were less affected by their proximity to major roads and highways, occurring all along the gradient, while swamp wallabies sharply decreased their numbers as the distance from the road increased.

Figure 11. Average numbers of red-necked wallaby (RNW) and swamp wallaby (SW) pellet groups between distance from major roads. RNW trend was significant (P = 0.0214, $F_{2,60}$ = 4.0991), as was SW trend (P = 0.0075, $F_{2,77}$ = 5.2141). ANCOVA did reveal a significant relationship (P = 0.0038, $F_{1,139} = 8.6532$).

 Red-necked wallabies displayed a nonlinear significant relationship with distance from urbanized areas (**Figure 12**). The concentration of pellet groups in each sample point increased as distance from urbanization increased from 0m to 5000m, past which point the average pellet group number peaked and began to decrease (as distance from urbanization continued to increase up to 9000m). Swamp wallabies also displayed a nonlinear significant trend with distance from urbanization. The average number of pellet groups in each sample peaked at 1000m from urban areas, and then decreased as distance from urbanization increased up to 6000m. The two species' responses to urbanized areas differed significantly from each other when compared, with rednecked wallaby pellet group averages increasing linearly with increasing distance from urbanization, and swamp wallaby averages decreasing linearly along the same spectrum.

Figure 12. Average numbers of red-necked wallaby (RNW) and swamp wallaby (SW) pellet groups between distance from heavy urbanization. RNW trend was significant (P = 0.0162, $F_{2,60}$ = 4.4185), as was SW trend (P = 0.0104, $F_{2,77}$ = 4.434). ANCOVA did reveal a significant relationship ($P = 0.0011$, $F_{1,139} = 11.1861$).

3.4 Habitat and land management status

Red-necked wallaby plots were classified into ten different habitat types: cleared and severely disturbed lands, dry sclerophyll forest, heath, heath swamp, non-native vegetation, southern tableland dry sclerophyll forest, Sydney montane dry sclerophyll forest, Sydney montane heath, wet sclerophyll forest, and southern tableland wet schlerophyll forest. The

highest average number of pellet groups was found in areas of non-native vegetation and cleared/severely disturbed areas, while the lowest was in the tableland dry sclerophyll forest

(**Figure 13**).

Figure 13. Distribution of red-necked wallaby pellet averages between habitat types. Letters represent averages that are significantly different from each other as determined by Student's t test.

Swamp wallaby plots were classified into seven different habitat types: tall Eucalypt

forest, mixed woodland, heath/scrub/swamp, low Eucalypt forest, modified bushland, open

Eucalypt forest, and open shrub canopy with dense groundcover of sedges and forbs. Student's t

test revealed no variance between any of the different types (**Figure 14**)

different from each other as determined by Student's t test; there was no variance in the swamp wallaby's preferences. **Figure 14.** Distribution of swamp wallaby pellet averages between habitat types. Letters represent averages that are significantly

Red-necked and swamp wallabies had significantly different responses to protected and non-protected lands. Red-necked wallaby pellets were found at a higher density in the protected areas compared to land under other management (a difference of 56%). Swamp wallaby pellets were found at a much higher density in land under other management than land within national parks and state forests (a difference of 75%). When compared with each other, swamp wallabies preferred "other" land to a difference of 66%, while red-necked wallabies overwhelmingly preferred protected land more than swamp wallabies (a difference of 68%).

Figure 15. Distribution of swamp and red-necked wallaby pellet averages between protected and non-protected land management statuses. Letters represent averages that are significantly different from each other as determined by Student's t test; swamp wallabies preferred non-protected lands, while red-necked wallabies were denser in the state forests and national parks.

4. Discussion

4.1 Habitat preferences

Red-necked wallabies and swamp wallabies overall displayed very different suites of topographic landscape preferences. Swamp wallabies were able to utilize broad ranges of elevation and water resources, as well as very steep slopes, while red-necked wallabies preferred flat areas and high elevations and seemed to avoid natural rivers and streams. The comparison between species' elevation preferences is skewed due to the simple difference in elevation of the study areas, but the data still show drastically different proportional relationships. The lack of significant trends in swamp wallaby pellet densities when correlated with each of these variables suggests that the swamp wallaby is not highly affected by any one of them, whereas the rednecked wallaby has stricter needs that it strives to meet.

 With regard to biotic and climate variables, red-necked wallabies displayed a curious pattern: while they seemed to avoid natural sources of water in the landscape, the average densities of their pellet numbers increased with the annual rainfall averages. Furthermore, they did not display a significant relationship with the Enhanced Vegetation Index numbers. These trends suggest that areas of high rainfall are preferred, but not because of the increase in vegetation cover that may accompany increased availability of water; instead, it is possible that rainfall and more non- or semi-permanent water sources would be used for drinking water, whereas permanent water sources such as streams and rivers are avoided for some other reason. Swamp wallabies seemed to have an ideal amount of annual rainfall at about 1300mm per year, although without a significant pattern relating to highly vegetated areas (the EVI mean results; see section 3.2), the reasons behind this ecological relationship are difficult to discern.

25

The patterns observed between densities of both species and the sites' fire history may be related to dietary preferences. Red-necked wallabies appeared to prefer areas that had not been burned recently much more than the swamp wallabies, while swamp wallabies themselves did not display any significant correlation. Di Stefano (2007) noted that cleared or burned areas generally create patches of early successional forest adjacent to mature stands, providing high quality foraging and shelter environments for many species. Bushfires increase the number of shrubs and potentially invasive species in an area, thickening the understory within a few years and maintaining it until the trees can grow tall enough to begin outcompeting the shrubs for sunlight. As a result, red-necked wallabies may find it harder to graze in more recently-burned areas, whereas swamp wallabies would have a plentiful amount of woody vegetation to sample and a large amount of cover.

4.2 Surviving in the urbanized environment

 Red-necked wallabies displayed a clear avoidance pattern related to all of the humandeveloped variables. When the border of protected land was considered, their pellet densities peaked at 2750 m into the state forest/national park area; when distance from the road was considered, pellet densities peaked at 3500 m; and when distance from built-up urbanized areas was considered, pellet densities peaked at 5000 m away. Furthermore, in areas between large urban sprawl and protected land, pellet densities decreased linearly as sites were sampled farther away from the protected border (and most often therefore closer to urbanization).

The small variation in peak distances within these patterns likely relates to the landscape matrix. Red-necked wallabies appear to avoid urban sprawl most strongly, thriving best 5000 m away, but major roads can extend outside urban sprawl and into this range, decreasing that distance to 3500 m. A third step further removed is the protected land border, and because that

26

land is already somewhat distanced from major urban environments, red-necked wallabies may not have to go deeply into the reserve to reach their ideal distance (resulting in the relatively small measure of 2750 m away from the border to the highest pellet density).

 Swamp wallabies, on the other hand, appeared to thrive closer to urbanized areas. Pellet densities dropped abruptly to zero with increasing distance into protected areas and away from human disturbance, and increased significantly as samples were taken closer to urbanized areas. Interestingly, there still appeared to be an "ideal distance" for the swamp wallabies from both roads and heavily-developed areas, which was around 1000 m—several times smaller than the red-necked wallaby's 5000 m.

4.3 Explanations for landscape-use patterns

 The data certainly support the previous research stating that swamp wallabies have been able to thrive on the fringes of urban environments (Ben-Ami 2005), and provide possible explanations for the differences in swamp wallaby and red-necked wallaby persistence. Rednecked wallabies preferred flat, high ground with grasses and open areas, such as the cleared and disturbed habitat, which reflects a pattern similar to results obtained by Le Mar and McArthur (2005) and Southwell (1987) in studies of red-necked wallaby habitat preference. Unfortunately, these are exactly the types of land that are developed by humans, as it is difficult to clear-cut and construct buildings on steep slopes. This overlap may have resulted in the red-necked wallaby's decline near urban areas, as it was pushed out of its ideal habitat and forced into the interior of protected non-developed land to seek it elsewhere. The factors involved in this "pushing out" remain ambiguous; however, they are likely directly related to the detrimental effects of development on surrounding ecosystems as discussed in section 1.2. A second possible explanation is that the red-necked wallaby was more directly "hunted" out as opposed to

indirectly nudged away from urbanized areas. As the Sydney area was developed, the beginnings of urbanization would have brought humans into close contact with this grazing species and provided easy opportunities to hunt them.

 Swamp wallabies, as a cryptic species and more of a generalist in both diet and habitat requirements (as noted in **Figure 14**) than red-necked wallabies, may have been better adapted to tackle the challenges of living next door to urbanized areas. Because they appear to be able to survive quite well on steep slopes and at varying elevations, moreso than red-necked wallabies, they would be able to take advantage of remnant vegetation that was unsuitable for human development. However, this does not explain why swamp wallaby pellet density decreased in this study with increasing distance from urbanized areas—if being a generalist species were the only factor, swamp wallabies should have been in every study site. It seems that there is another reason at work here that may actually be drawing swamp wallabies to the urban fringe, which is not clear in the context of this study. Ben-Ami (2005) detected a similar pattern in the distribution of swamp wallabies in Muogamarra Nature Reserve 50 km north of Sydney, and suggested that they may be drawn to the exotic vegetation found in human gardens as a food source. Several other studies in the past have also demonstrated that swamp wallabies prefer environment edges near previously-cleared habitat, usually with the authors suggesting that abundance of food is greater than in the forest interior (Floyd 1980, Di Stefano et al. 2009).

4.4 The future of urban impacts on species persistence

 Unfortunately, success on the urban fringe or retreat into protected habitats do not guarantee survival of red-necked and swamp wallabies as human infrastructure continues to encroach upon the natural world. Swamp wallabies persisting in urban areas are increasingly falling victim to vehicle collisions as they attempt to disperse across roadways (Ramp and Ben-

28

Ami 2006) and their survival thus far may be compromised if they continue to be actively drawn to human-impacted areas. Meanwhile, the red-necked wallaby may also continue to be driven into the interior of remnant vegetation; depending on its degree of specialization, it may not be able to recover if the species integrity continues to be stressed.

5. Conclusions

 This study supported the theory that red-necked and swamp wallabies respond differently to urbanization and human development. The two species demonstrated very different patterns and preferred distances from heavily built-up areas, major roads, and protected land areas, with red-necked wallabies favoring avoidance behavior and swamp wallabies favoring attraction. These two wallaby species also have many dissimilar life history traits that may contribute to this difference, including diet breadth, social organization, and preferred habitats.

 As the human population continues to grow, so too will its infrastructure and resource needs, and by extension its impact on the surrounding environment. Urban planning and land management need to incorporate landscape-scale studies and behavioral ecology studies both into biodiversity conservation measures. Without this holistic approach, species such as the rednecked wallaby that overlap with humans in terms of habitat needs will suffer, and species such as the swamp wallaby that can still persist on the fringes of the urban world may reach their limit and begin to decline. This pattern can be extended to other wildlife, as well: generalist species that have been able to persist thus far are not completely removed from stress, and must be considered as resistant only to a certain degree, while the needs of specialist species must also be considered and accounted for in development planning.

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