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Heterogeneous wetland complexes, buffer zones, and travel corridors: Landscape management for freshwater reptiles

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ABSTRACT

While the importance of nearby terrestrial habitats is gaining recognition in contemporary wetland management strategies, it is rarely recognized that different wetlands are often diverse in their functions of meeting the annual or life-cycle requirements of many species, and that migration between these wetlands is also critical. Using radio-telemetry, we examined terrestrial habitat use and movements of 53 eastern long-necked turtles (*Chelodina longicollis*) in an area of southeast Australia characterized by spatially diverse and temporally variable wetlands. Male and female *C. longicollis* exhibited a high degree of dependence on terrestrial habitat, the majority (95%) of individuals using sites within 375 m of the wetland. Turtles also associated with more than one wetland, using permanent lakes during droughts and moving en masse to nearby temporary wetlands after flooding. Turtles used 2.4 ± 0.1 (range = 1–5) wetlands separated by 427 ± 62 (range = 40–1470) m and moved between these wetlands 2.6 ± 0.3 (range = 0–12) times over the course of a year. A literature review revealed that several species of reptiles from diverse taxonomic groups move between wetlands separated by a mean minimum and maximum distance of 499–1518 m. A high proportion of studies attributed movements to seasonal migrations (55%) and periodic drought (37%). In such cases we argue that the different wetlands offer complimentary resources and that managing wetlands as isolated units, even with generous terrestrial buffer zones, would not likely conserve core habitats needed to maintain local abundance or persistence of populations over the long term. Core management units should instead reflect heterogeneous groups of wetlands together with terrestrial buffer zones and travel corridors between wetlands.

1. Introduction

Wetland losses and declines in associated faunal communities worldwide (Dahl, 1990; Richter et al., 1997; Finlayson and Rea, 1999) challenge conservation biologists with developing biologically relevant management actions that will prevent further endangerment of wetland communities and provide a framework for their recovery. Contemporary management strategies include establishing wetland reserves (e.g., Ramsar Convention), identifying and protecting keystone wetlands for particular taxa (e.g., North American Waterfowl Management Plan, US Fish and Wildlife Service, 1986), and replacing wetlands lost through land development (e.g., mitigation banking, National Research Council, 2001). Because terrestrial habitats surrounding wetlands play an integral role in regulating microclimate and inputs of nutri-

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ents, sediments, and pollutants, it is generally recognized (though not always practiced) that managing a terrestrial buffer zone within 30–60 m of the wetland is vital to maintaining wetland quality (Semlitsch and Bodie, 2003). While the above strategies may adequately conserve the quality of selected wetlands, they have been criticized as focussing too narrowly on the wetland as an individual patch and de-emphasizing the functional linkages of the wetland with other wetlands and the wider landscape (Amezaga et al., 2002).

Criticism of the wetlands-as-patches approach to management derives primarily from an understanding that ecological processes regulating wildlife populations often depend on both patch quality and the structure of the wider landscape. For instance, Semlitsch and Bodie (2003) review the literature on habitat use in semi-aquatic amphibians and reptiles and suggest that core terrestrial zones should extend up to 289 m beyond the delineated wetland boundary to maintain terrestrial resources used by species for critical life-history functions, and an additional 50 m should be added to provide a buffer against edge effects. While Semlitsch and Bodie (2003) make important advances by expanding upon the focus of wetland management to include terrestrial habitats used by wildlife beyond the narrow strip immediately surrounding the wetland, their recommendations are still directed at individual wetlands as the management units, albeit larger and more comprehensive units. Such a strategy neglects the importance of other wetlands in the landscape and the quality of travel routes between them.

Where wetlands in a region are spatially diverse or temporally variable, wildlife may require the use of several different wetlands during a season or lifetime (Haig et al., 1997; Joyal et al., 2001; Naugle et al., 2001; Roe et al., 2003, 2004). For these species and those that interact as metapopulations, where dispersal between wetlands is vital for maintaining regional population stability (Harrison, 1991), characteristics such as the availability, proximity, quality, and heterogeneity of other wetlands in the landscape and the facility with which individuals can travel among them (landscape connectivity) are all likely to influence demographic processes (Gibbs, 2000; Marsh and Trenham, 2001). These are fundamental concepts in landscape and wildlife ecology (Dunning et al., 1992; Taylor et al., 1993) that have not been sufficiently conveyed across disciplines (e.g., to wetlands scientists and policy makers; Cushman, 2006). Consequently, it comes as no surprise that land managers rarely consider landscape context when making decisions regarding management of aquatic wildlife.

Our aim was to determine whether management that considers wetlands as individual units, either as isolated aquatic patches or in conjunction with terrestrial buffer zones, would be sufficient for the freshwater turtle *Chelodina longicollis* in southeastern Australia. Specifically, we examine details of terrestrial habitat use around wetlands as well as movements by individuals among different types of wetlands. As previous studies have described several types of freshwater wetlands that differ widely between one another and over time according to temporal variation in rainfall at our study site (Georges et al., 1986; Kennett and Georges, 1990; Norris et al., 1993), we hypothesized that turtles of both sexes would associate with more than one wetland to meet annual needs. Furthermore, to bridge the gap between wildlife ecology and environmental management practices and policy, we summarize the literature on inter-wetland movements for wetland reptiles to assess the incidence of this behavior, its functions, and the spatial scales over which individuals typically travel. Such information for a broad range of wetland reptiles is needed to determine biologically relevant management strategies.

2. Methods

2.1. Study site

We studied turtles from September 2004 to March 2006 in Booderee National Park, a 7000 ha reserve located within the Commonwealth Territory of Jervis Bay in southeast Australia (150°43′ E, 35°09′ S). Kennett and Georges (1990) and Norris et al. (1993) provide a detailed description of the study site. The site is characterized by a mosaic of freshwater habitats including several permanent dune lakes, a network of permanent and ephemeral streams, and a number of temporary swamps of various hydroperiods (duration of surface water presence). Hereafter, we refer to all aquatic habitats as wetlands, and each wetland was defined as either permanent or temporary based on whether it was observed to have dried during the course of our study or from examination of recent aerial photographs. Typical wetland plant species at our site include *Baumea articulata*, *Eleocharis sphacelata*, *Leptospermum juniperinum*, and *Schoenus brevifolius*. These wetlands occur within forests dominated by *Eucalyptus pilularis*, *Eucalyptus gummifera*, *Eucalyptus botryoides*, *Eucalyptus paniculate*, *Eucalyptus sclerophylla*, *Banksia serrata*, *Banksia integrifolia*, *Melaleuca linariifolia*, and heath scrubland dominated by *Allocasuarina distyla*, *Banksia ericifolia*, *Hakea teretifolia*, *Sprengelia incarnata*. The geology consists of sandstone covered by varying depths of sand.

We used digitized maps describing the distribution of terrestrial and aquatic habitats in the study area adapted from those of N. Taws (in litt.). Wetlands were classified as either permanent or temporary (as described above), and all non-aquatic habitats were collapsed into a single category and classified as terrestrial. We refined the mapping of some wetlands based on our assessment of wetland/terrestrial boundaries, and added other small wetlands (0.10 ha, representing the smallest habitat patch size on our maps) not easily identified from aerial photographs. Because many wetlands have fluctuating water levels, we defined the wetland edge as the interface of the temporarily flooded zone and terrestrial habitat. All habitat edges were drawn from aerial photographs and ground-truthed with a GPS unit (GPS III Plus, Garmin Corp., Olathe, Kansas) with an error of 1–7 m.

2.2. Data collection

We captured turtles using baited crab traps or by hand from eight different wetlands from three sets of wetland complexes (Lake McKenzie, Ryan's Swamp, and surrounding wetlands; Blacks Waterhole and surrounding wetlands; and Steamers Waterholes). We fitted 53 adult turtles (32 F, 21 M) with radio-transmitters (Sirtrack Ltd., Havelock North, New Zealand) mounted on aluminium plates and secured to the carapace with bolts or plastic ties through holes drilled in the rear marginal scutes. Initial plastron length and mass of females was 158.3 ± 1.7 mm (mean ± SE) and 691 ± 22 g, and for males 140.5 ± 5.7 mm and 512 ± 15 g. Transmitters ranged from 2.5% to 6.1% of the turtle's body mass.

We located turtles three to four days per week from September to March (active season) during each year of the study, and once per month from April to August (inactive season). At each location, we determined the coordinate position using GPS units held directly above the turtle or from estimated distance and bearing measurements to known points (e.g., triangulation) when the turtle could not be closely approached. We then plotted location coordinates on habitat maps using ArcView GIS 3.1 (Environmental Systems Research Institute, 1992). We also classified each location as being in either a terrestrial habitat or wetland. We calculated the proportion of locations in terrestrial habitats, terrestrial duration (the number of consecutive days spent in terrestrial habitats without returning to water), the number of movements to terrestrial refuge sites (defined as a movement away from a wetland where a turtle remained for at least five days before returning to the wetland), and the mean and maximum distance from terrestrial locations to the nearest wetland for each turtle. We also noted wetland type (either permanent or temporary) for each location, and measured straight-line distance to the nearest wetland edge for terrestrial locations. We quantified the total number of wetlands visited, the number of times movements between wetlands occurred (hereafter referred to as inter-wetland movements), and overland distances travelled between wetlands for each turtle. Wetlands were only considered distinct if they were isolated from each other by terrestrial habitat. We measured distances between wetlands and between terrestrial locations and the nearest wetland using the Nearest Features extension for Arc View GIS.

2.3. *Statistical analyses*

Although the main focus of this investigation was to determine the frequency and spatial scale of terrestrial habitat use and movements among different types of wetlands for *C. longicollis*, we nevertheless examined whether the sexes differed in their movements and behavior. We performed all statistical analyses with SPSS Version 11.5 (1999). Where appropriate, we examined the assumptions of homogeneity of variances and normality; when data failed to meet assumptions, data were transformed to approximate normal distributions or equal variances. We used non-parametric tests when both raw and transformed data deviated significantly from normal distributions or equality of variances. Statistical significance was accepted at the $\alpha = 0.05$ level.

To determine if the sexes differed in the number of wetlands used, frequency of inter-wetland movements, number of temporary wetlands used, proportion of locations in terrestrial habitats, or the number of movements to terrestrial refuge sites, we used Mann–Whitney *U* tests. Additionally, we examined whether density of wetlands within a buffer radius of 1470 m (the longest inter-wetland movement observed in this study; see results) of the wetland of original capture influenced the number of wetlands used or the number of inter-wetland movements using linear regression. We used analysis of variance (ANOVA) to examine whether the sexes differed in overland distances travelled between wetlands. To examine differences between the sexes in terrestrial duration and mean and maximum distances from terrestrial refuge sites to the nearest wetland, we used MANOVA. All distance variables, terrestrial duration, and number of wetlands used were $\log_{10}$-transformed prior to analyses, and number of inter-wetland movements was square root-transformed.

3. Results

Individual turtles were radio-tracked for 336 ± 23 (mean ± SE) consecutive days throughout which we obtained 79 ± 4 locations per individual. Individuals used terrestrial habitats extensively for periods of extended refuge, but males and females did not differ significantly in any aspect of terrestrial habitat use examined (Table 1, Fig. 1). Ninety-one percent of males and 75% of females used terrestrial habitats at some point during the study, and individuals that did so used terrestrial habitats for 28 ± 4% (range = 1–99%) of their locations where they stayed for 64 ± 14 (range = 1–480) consecutive days without returning to wetlands. The majority of terrestrial locations were in forests where individuals were either completely buried under detritus and sand or with a small portion of the carapace exposed. Although we did not locate turtles every day, estimates of terrestrial duration are likely accurate given that in most cases there was rarely any indication that individuals moved from terrestrial refuge sites, and terrestrial habitat use was mostly associated with wetland drying (i.e., turtles would have to travel to distant wetlands and back in a short time). Turtles travelled 99 ± 13 (range = 6–505) m from the nearest wetland, with 95% of terrestrial locations within 375 m of the nearest wetland (Fig. 2).

Table 1 – Terrestrial habitat use by a freshwater turtle, Chelodina longicollis, in Booderee National Park, Australia

Variable	Female		Male		Test statistic	*p*
	Mean ± SE	Range	Mean ± SE	Range		
Terrestrial locations (%)	22 ± 5	0–99	24 ± 6	0–73	−0.563	0.574
Movements to terrestrial refuge (n)	0.84 ± 0.20	0–3	1.33 ± 0.30	0–4	−1.269	0.204
Terrestrial duration (days)	70 ± 22	1–480	55 ± 17	1–229	1.527	0.223
Mean distance to nearest wetland (m)	116 ± 20	20–390	77 ± 16	6–223	1.527	0.223
Max distance to nearest wetland (m)	208 ± 34	27–505	147 ± 36	6–457	1.527	0.223

See methods for statistical analyses used.

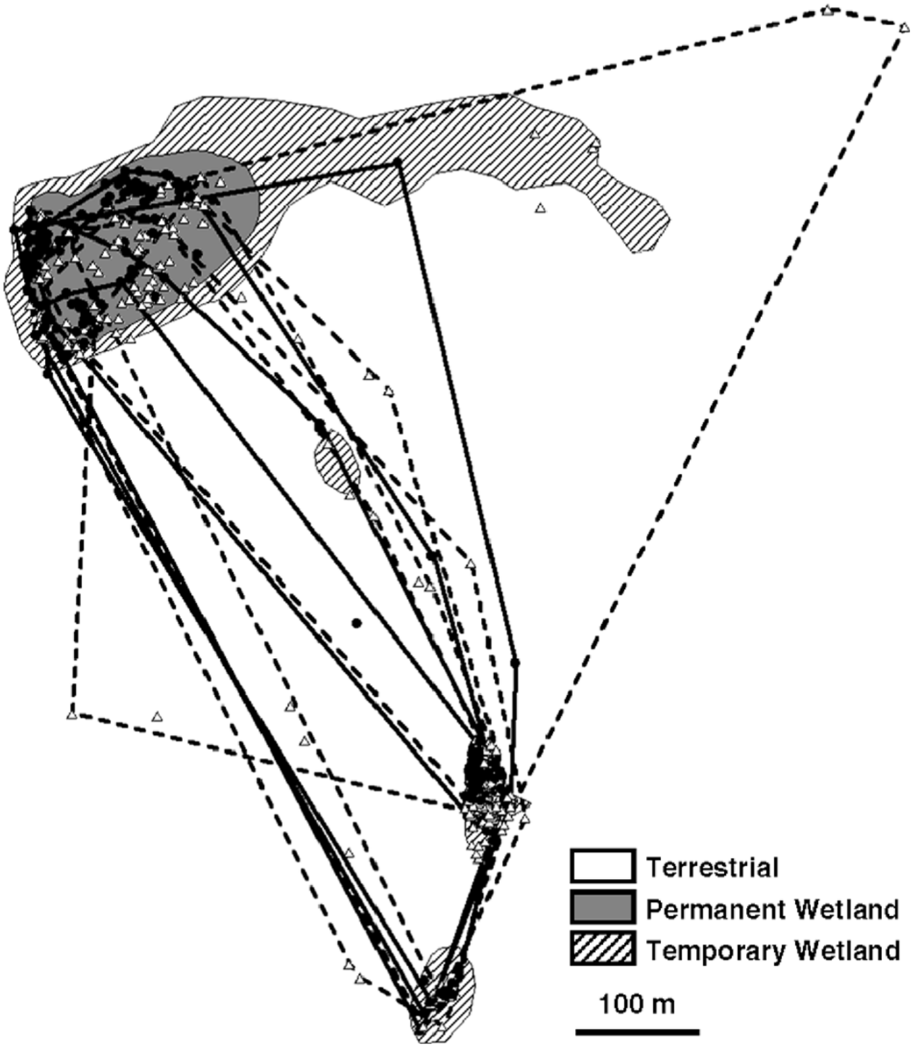

Fig. 1 – Locations and minimum convex polygons for *Chelodina longicollis* males (circles and solid lines) and females (triangles and dashed lines) studied by radio-telemetry at a wetland complex in Booderee National Park, Australia. Note that we show the movements of individuals at only one of three wetland complexes (Blacks Waterhole and surrounding wetlands), but patterns of movement among wetlands were similar at the other sites.

Most individuals maintained an association with several temporary ponds or streams, in addition to a permanent dune lake (Table 2, Fig. 1). However, males and females did not differ significantly in any aspect of wetland movements examined (Table 2). Seventy-six percent of males and 81% of females maintained an association with more than one wetland, with individuals using 2.4 ± 0.1 (range = 1–5) different wetlands, moving between these wetlands 2.6 ± 0.3 (range = 0–12) times, and travelling 427 ± 62 (range = 40–1470) m overland between wetlands. Wetland density surrounding the eight different wetlands where turtles were originally captured ranged from 1.29 to 2.45 wetlands/km^2, but had no influence on the number of wetlands used ($R^2 = 0.001$, $P = 0.789$) or number of inter-wetland movements ($R^2 = 0.005$, $P = 0.615$).

4. Discussion

Our study demonstrates that both male and female *C. longicollis* use terrestrial habitats far from wetlands for extended durations and maintain associations with several wetlands of different types over the course of a year, even when wetlands are widely dispersed. Terrestrial habitats are important sites of refuge and groups of wetlands, not individual wetlands, should be considered together as harbouring local populations. Consequently, management schemes directed at wetlands as individual units with only narrow terrestrial buffer zones would not adequately capture the mosaic of habitats used by this species.

The inclusion of wide terrestrial buffer zones in wetland management recommended by many researchers (reviewed in Semlitsch and Bodie, 2003) denotes an important shift in focus from wetlands as isolated patches to a more inclusive definition of what constitutes core habitat for wetland wildlife. Although the 127–289 m terrestrial core zones recommended by Semlitsch and Bodie (2003) for reptiles should not be considered canonical, such a zone would nevertheless encompass a large proportion (71–89%) of terrestrial habitats used by the *C. longicollis* population in this study (Fig. 2). For inclusion of 95% of *C. longicollis* terrestrial habitats, a consid-

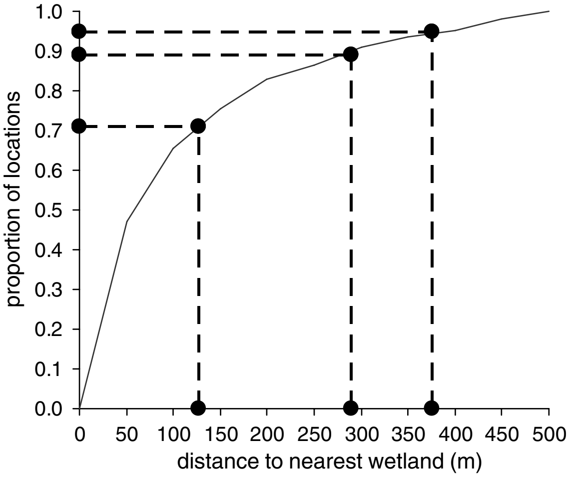

Fig. 2 – Proportion of terrestrial locations within various distances of the nearest wetland edge for *Chelodina longicollis*. The vertical and horizontal dashed lines represent the proportion of locations that would be included in the minimum (127 m) and maximum (289 m) terrestrial buffer zones recommended by Semlitsch and Bodie (2003) for reptiles. For reference, the distance that would include 95% of terrestrial locations is also indicated.

erably larger 375 m zone would be required (Fig. 2). That nearly every turtle used terrestrial habitats where they remained for extended durations indicates terrestrial habitat served important functions including temporary refuge when wetlands dried, nesting, and overwintering. However, while managing wetlands and adjacent terrestrial buffer zones as a single habitat unit may succeed for animals that remain philopatric to a single wetland, the habitat requirements of species that maintain associations with more than one wetland would continue to be neglected.

C. longicollis associates with several wetlands over the course of a year, but movements between wetlands are not specific to this species. Our literature review revealed that at least 19 species of turtles, 5 species of snakes, and 1 species of crocodilian from 18 US states and 7 countries maintain associations with more than one body of water, sometimes making frequent trips between wetlands (Table 3). Reptiles using more than one wetland typically travel among two or three wetlands (full range = 2–9) separated by a mean minimum and maximum distance of 499–1518 m (full range 10–8500 m; Table 3). It could be argued that individuals may move between wetlands simply because several wetlands are available in some areas and populations could subsist in high abundance even when confined to using only a single wetland. While this may be true in some cases, the majority (55%) of studies documenting inter-wetland movements in reptiles attribute such movements to seasonal migrations (e.g., between active season and overwintering sites, wetlands that seasonally flood and dry), 42% note reproduction (mating, nesting, parturition), 37% specify movements from drying wetlands due to periodic drought, and 32% attribute movements to exploitation of alternate foraging sites (Table 3). We conclude that movements between wetlands allow individuals of several species to carry out many essential behaviors and such movements would likely continue even if long distances must be traversed.

We found that *C. longicollis* continued to move among groups of wetlands with similar frequency in areas representing a gradient from low to high wetland density (1.29–2.45 wetlands/km^2). Although wetland densities spanned only a small range at our site, the continued movements among wetlands where wetlands were most widely dispersed (up to 1470 m) suggests that movements between wetlands are not a simple artefact of the availability of nearby wetlands, but instead that migration served an important function. Previous studies demonstrate that *C. longicollis* in temporary wetlands exploit abundant prey resources in the absence of competitors, grow faster, and have substantially higher reproductive output than when in permanent lakes, but individuals must ultimately migrate back to the less productive permanent lakes to withstand extended dry periods (Kennett and Georges, 1990). Because the lakes at our site are low in productivity, invertebrate and vertebrate food resources, and have established populations of competitors typical of permanent waterbodies (e.g., fish), should the turtles be confined to the permanent lakes alone, the regional population would likely decline as the lakes alone can only support low densities of carnivorous turtles (Kennett and Georges, 1990; Norris et al., 1993). Evidence for such declines comes from Kennett and Georges (1990) observations of many emaciated turtles in the lakes after a long drought when temporary wetlands did not flood, and our observation of high mortality (105 individuals over 17 months) in one permanent lake during a period of low rainfall when many turtles had left the dry temporary wetlands to return to the lake. Alternatively, if the turtles are confined to using only the temporary wetlands, the population would not persist following extended drought as individuals cannot remain in terrestrial habitats indefinitely without returning to water (Chesseman, 1978). Thus, the combination of several permanent and temporary wetlands is a key landscape element contributing to

Table 2 – Wetland use by a freshwater turtle, Chelodina longicollis, in Booderee National Park, Australia

Variable	Female		Male		Test statistic	*p*
	Mean ± SE	Range	Mean ± SE	Range		
Wetlands used (n)	2.3 ± 0.2	1–4	2.4 ± 0.3	1–5	−0.190	0.849
Inter-wetland movements (n)	2.6 ± 0.4	0–9	2.7 ± 0.6	0–12	−0.259	0.796
Inter-wetland movement distance (m)	388 ± 76	40–1147	489 ± 107	70–1470	1.222	0.276
Temporary wetlands used (n)	1.5 ± 0.1	0–3	1.9 ± 0.2	1–4	−1.026	0.305

See methods for statistical analyses used.

Table 3 – Summary of inter-wetland movements for wetland reptiles

Species, location (*n*)	Wetlands used	Movement frequency	Distance travelled	Sex	Data source, reasons for movement, and methods
Turtles					
Apalone ferox, Florida (13)	2	–	50–2100	–	Aresco, 2005[a,f,g]
Chelodina longicollis, Australia (25)	2	–	800–2500	M, F	Kennett and Georges, 1990[a,b,f]
Chelodina longicollis, Australia (11)	2	–	193–789	M, F	Stott, 1987[g,h]
Chelodina longicollis, Australia (53)	1–5 (2.4)	0–12 (2.6)	62–1470 (427)	M, F	This study[a,b,c,e]
Chelydra serpentina, Canada (2)	2	–	500	F	Obbard and Brooks, 1980[d,f]
Chelydra serpentina, South Carolina (1)	2	–	10	M	Gibbons, 1970[f,g]
Chrysemes picta bellii, Nebraska (12)	2	–	2100	–	McAuliffe, 1978[b,c,f]
Chrysemes picta bellii, Iowa (4)	2	–	–	–	Christiansen and Bickham, 1989[a,f]
C. p. marginata, Michigan (6)	1–2	–	125	M, F	Rowe, 2003[e]
C. p. marginata, Michigan (600)	2	–	550–1200	M, F	Scribner et al., 1993[f,g]
C. p. picta, Virginia (259)	1–2	0–2	230–3300	M, F	Bowne et al., 2006[a,e,f]
Clemmys guttata, Maine (16)	1–4 (2.3)	–	110–1150 (311)	F	Joyal et al., 2001[c,d,e,f]
Clemmys guttata, Massachusetts (9)	2–3	2	120	M, F	Graham, 1995[b,c,e]
Clemmys guttata, Massachusetts (26)	1–3	–	20–550	M, F	Milam and Melvin, 2001[b,c,e]
Clemmys guttata, Connecticut (8)	2	–	250	M, F	Perillo, 1997[b,c,e]
C. muhlenbergii, Virginia (31)	1–2	0–4	200–530	M, F	Carter et al., 2000[e]
Deirochelys reticularia, Virginia (5)	1–9	–	250–600	M, F	Buhlmann, 1995[b,d,e]
Deirochelys reticularia, South Carolina (3)	2	–	10	M	Gibbons, 1970[f,g]
Deirochelys reticularia, South Carolina (7)	2	–	515–8500	M, F	Buhlmann and Gibbons, 2001[a,c,d,f,g]
Emydoidea blandingii, Maine (12)	1–6 (2.8)	–	90–2050 (680)	M, F	Joyal et al., 2001[d,e,f]
Emydoidea blandingii, Minnesota (25)	1–6	0–5 (1.6)	77–2900 (533)	M, F	Piepgras and Lang, 2000[c,d,e]
Emydoidea blandingii, Illinois (23)	2	–	170–1400	M, F	Rowe and Moll, 1991[d,e,f]
Emys orbicularis, Italy (7)	1–2	0–2	600	F	Rovero and Chelazzi, 1996[d,e]
Emys orbicularis, Italy (–)	2	–	200	–	Lebberoni and Chelazzi, 1991[b,f]
Emys orbicularis, Germany (4)	1–3	0–3	200–600	F	Schneeweiss and Steinhauer, 1998[d,e]
Graptemys flavimaculata, Mississippi (26)	1–2	–	100	F	Jones, 1996[b,d,e]
Kinosternon baurii, Florida (15)	2	–	35–50	M, F	Wydoga, 1979[c,f,g,h]
Kinosternon flavescens, Oklahoma (1)	2	–	610	–	Mahmoud, 1969[c,f]
Kinosternon leucostomum, Belize (6)	2	–	200	–	Moll, 1990[c,f]
Kinosternon scorpioides, Belize (3)	2	–	200	–	Moll, 1990[c,f]
Kinosternon sonoriense, New Mexico (2)	2	–	1500	–	Ligon and Stone, 2003[f]
Kinosternon subrubrum, Florida (7)	2	–	50–2100	–	Aresco, 2005[a,f,g]
Kinosternon subrubrum, South Carolina (1)	2	–	10	M	Gibbons, 1970[f,g]
Kinosternon subrubrum, South Carolina (1)	2	–	440–515	M, F	Buhlmann and Gibbons, 2001[a,c,d,f,g]
Pseudemydura umbrina, Australia (–)	2	–	500	–	Burbidge, 1981[c,e]
Pseudemys floridana, Florida (236)	2	–	50–2100	–	Aresco, 2005[a,f,g]
Pseudemys floridana, South Carolina (5)	2	–	3000	M, F	Buhlmann and Gibbons, 2001[a,c,d,f,g]
Trachemys scripta, South Carolina (2)	2	–	10	M	Gibbons, 1970[f,g]
Trachemys scripta, South Carolina (14)	2	–	3000–5500	M, F	Buhlmann and Gibbons, 2001[a,c,d,f,g]
Trachemys scripta, South Carolina (11)	2	–	400	–	Gibbons et al., 1983[a,f,g]
Trachemys scripta, South Carolina (178)	2	–	200–6000	M, F	Gibbons et al., 1990[a,c,d,f,g]
Trachemys scripta, Mississippi (39)	2	–	600–1100	M, F	Parker, 1984[b,d,f]
Trachemys scripta, Florida (119)	2	–	50–2100	–	Aresco, 2005[a,f,g]
Snakes					
Liasis fuscus, Australia (25)	2	0–2	2000–5000	M, F	Madsen and Shine, 1996[b,c,e]
Nerodia sipedon, Ohio/Michigan (13)	1–4 (2.1)	0–13 (2.8)	17–331 (97)	M, F	Roe et al., 2003, 2004[c,d,e]
Nerodia erythrogaster neglecta, Ohio/Michigan (15)	1–7 (4.1)	0–45 (9.1)	15–1013 (143)	M, F	Roe et al., 2003, 2004[b,c,e]
Thamnophis elegans, California (4)	2	–	1400–3000	–	Kephart, 1981[f]
Thamnophis sirtalis, California (2)	2	–	1700	–	Kephart, 1981[f]

Table 3 – *continued*

Species, location (*n*)	Wetlands used	Movement frequency	Distance travelled	Sex	Data source, reasons for movement, and methods
Crocodilians					
Caiman crocodilus, Venezuela (20)	2	–	35–1050	–	Gorzula, 1979[c,f]

The number of wetlands used, frequency of movement between wetlands, and straight-line overland distances moved by individuals are reported as either single values or ranges and (means) where available.

Movements to other wetlands were considered to have occurred only if individuals were observed in two or more different wetlands, and if wetlands were separated by terrestrial habitats. These distinctions exclude documented immigration/emigration where either the source or destination wetlands were unknown, and movements that exclusively followed aquatic connections (i.e., streams, canals).

a Movements associated with periodic drought.
b Foraging.
c Seasonal migrations (e.g., between active season and overwintering sites, areas that seasonally flood and dry).
d Reproduction (mating, nesting, parturition).
e Radio-telemetry.
f Aquatic captures of marked individuals.
g Terrestrial drift fence.
h Spool-tracking.

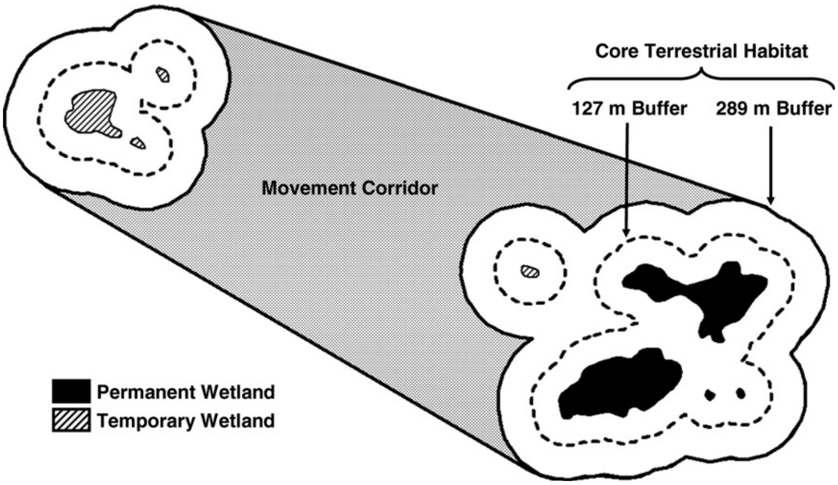

Fig. 3 – A stratified approach to landscape management for wetlands that considers heterogeneous groups of wetlands as the management units, along with buffer zones of 127 to 289 m to protect terrestrial habitat areas as recommended by Semlitsch and Bodie (2003), plus a broader terrestrial movement corridor where barriers to movement and sources of mortality are identified and mitigated while still allowing for sustainable land uses in this area.

regional carrying capacity, but this dynamic depends on the availability of both types of wetlands and the ability of turtles to migrate between them. For animals that migrate between wetlands to meet seasonal requirements or for those that must occasionally disperse to other wetlands to escape periodic environmental perturbations (e.g., extended drought), we argue that different wetlands offer complimentary (i.e., non-substitutable) resources. In such cases, not only must groups of wetlands comprise the relevant population units for management (Haig et al., 1997; Joyal et al., 2001; Naugle et al., 2001; Roe et al., 2003), but managers should also maintain wetland complexes reflecting the different types of naturally occurring wetlands in the region.

Together with maintenance of heterogeneous wetland complexes, landscape connectivity (the degree to which a habitat facilitates or impedes movement; Taylor et al., 1993), should be considered in wetland management. Maintaining terrestrial landscapes for connectivity may be a fundamentally different proposition than managing habitats immediately adjacent to wetlands (i.e., as a terrestrial buffer zone), as the quality of terrestrial habitat required for successful long-distance travel may be different that than required for other behaviors. Wetland reptiles seek very specific microclimate and structural conditions in terrestrial habitats for overwintering (Kingsbury and Coppola, 2000; Roe et al., 2003), aestivation (Morales-Verdeja and Vogt, 1997; Buhlmann and Gibbons, 2001), and nesting (Spencer and Thompson, 2003), all of which typically occur within 289 m of wetlands (Semlitsch and Bodie, 2003). In these areas, stringent restrictions on particular land use practices such as residential development, agriculture, and forestry would likely be necessary. Where wetlands are spatially clustered, terrestrial buffer zones may also include habitats used for travel between wetlands, but when wetlands are dispersed across greater distances, much of the habitat used for inter-wetland movements would be excluded (Fig. 3). Landscape management practices aimed at maintaining overland travel beyond the buffer zone areas may only require that habitats outside these zones remain permeable and offer safe passage for wildlife. For instance, roads are an example of a widespread terrestrial landscape modification that disrupts landscape connectivity, either as a behavioral barrier or as a mortality sink when roads bisect travel routes between wetlands (Dodd et al., 2004; Aresco, 2005), even on reserves designated for aquatic wildlife conservation (Bernardino and Dalrymple, 1992; Ashley and Robinson, 1996). Sources of mortality and movement barriers for wildlife along terrestrial travel routes could be identified and modified to mitigate their effects (e.g., fences and culverts; Dodd et al., 2004; Aresco, 2005), while still allowing for other land uses in these areas. Such a stratified approach to management, where zones of allowable land use are set by their likely impact on animals when using these zones, may be an effective way to strike a balance between the competing goals of wildlife conservation and land use (deMaynadier and Hunter, 1995; Semlitsch and Bodie, 2003; Fig. 3).

5. Conservation and management implications

Reptile populations have been severely impacted by landscape changes, and while commonly lumped together with amphibians as “herpetofauna”, reptiles have their own set of unique characteristics that warrant their consideration apart from amphibians in management decisions (Gibbons et al., 2000). Most amphibians are characterized as being philopatric to a single wetland and nearby terrestrial habitat (with the exception of juvenile dispersal; Marsh and Trenham, 2001), but our study demonstrates that many species of reptiles, including *C. longicollis*, may also move widely about the landscape maintaining associations with several types of wetlands to meet their life-cycle or seasonal requirements. Thus, it is not surprising that landscape characteristics such as forest cover, availability of other wetlands, and road density have all been identified as significant predictors of species persistence and local abundance for wetland reptiles at distances ranging from 250 to 2000 m from focal wetlands (Findlay and Houlahan, 1997; Joyal et al., 2001; Ficetola et al., 2004; Marchand and Litvaitis, 2004; Attum et al., in press).

Managing landscapes for high quality wetlands and large core terrestrial habitats adjacent to wetlands is an important step in a landscape approach to wetland management (Semlitsch and Bodie, 2003), but we argue that two additional measures, (1) maintaining the natural heterogeneity of wetland complexes and (2) provision of permeable travel corridors among wetlands, would ultimately strengthen the success of conservation strategies for wetland reptiles. At our site a terrestrial core protection zone extending 425 m from wetlands would encompass 95% of terrestrial habitat used by *C. longicollis* as well as a buffer from edge effects. We also identified several important overland movement corridors, and this information was used in addressing the impact of roads on turtle migration in the park, and in designing a predator-exclusion fence (surrounding a lake) for the European red fox (*Vulpes vulpes*) that remained permeable to turtles travelling between wetlands (N. Dexter pers. com.). In the absence of species- or site-specific information, management can be guided by all-encompassing mean minimum and maximum values of habitat requirements derived from what is currently known for the taxon in question (e.g., for reptiles: Semlitsch and Bodie, 2003; this study). Ultimately, conservation planning should extend beyond localized groups of wetlands and surrounding terrestrial habitats to consider connectivity among groups of wetland complexes to allow for inter-population movements that maintain the long-term regional viability of populations via dispersal (Semlitsch and Bodie, 2003; Cushman, 2006). As wetland landscapes continue to become less dense and more homogeneous (Bedford, 1999; Brock et al., 1999; Gibbs, 2000), and as habitats between wetlands become increasingly fragmented and inimical, changing from an individual wetland to a landscape approach to managing wetland biodiversity should be of great concern to conservationists.

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