Temporal and spatial variation in landscape connectivity for a freshwater turtle in a temporally dynamic wetland system

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Abstract. Inter-wetland connectivity, defined here as the movement of biota among discrete water bodies, can have important population- and community-level consequences in aquatic systems. We examined inter-wetland connectivity in a southeastern Australian national park by intensively monitoring the movements of freshwater turtles (*Chelodina longicollis*) via capture–mark–recapture over a three-year period, and more sporadically for 25 years. A high percentage (33%) of turtles moved between wetlands, suggesting that single wetlands should not represent the minimum habitat unit harboring a *C. longicollis* population. Distance was the only structural landscape metric correlated with inter-patch transition probability, with probability declining as inter-wetland distance increased. Movements also appear to be strongly influenced by shifting resource quality gradients between temporary wetlands and permanent lakes according to drought and flood cycles, a pattern more consistent with migration between critical resource patches than occasional interpopulational dispersal. Rare dispersal events of up to 5.2 km were known to occur. Captures at a terrestrial drift fence suggest that small and immature turtles moved between wetlands more frequently than our aquatic sampling indicated. We caution that measures of actual (or functional) connectivity can be biased by sampling methods and the temporal scale of sampling and must also be interpreted in the context of factors that motivate animal movements. This requires some understanding of spatial and temporal variation in intra-patch processes (e.g., quality and extent) and the expected movement responses of animals (e.g., habitat selection) over extended time frames, information that can potentially yield more important insight on connectivity than measures of landscape structural features alone.

Key words: Chelodina longicollis; *drought; eastern long-necked turtle; habitat quality; inter-patch movement; metapopulation; migration; movement probability; multistate model; southeastern Australia; survivorship; wetland conservation.*

Introduction

Connectivity is a measure of the degree to which the landscape impedes or facilitates movement among patches (Taylor et al. 1993). Connectivity is most accurately assessed from the observed movements of individuals (i.e., actual or functional connectivity) as opposed to structural or potential connectivity, where movements are predicted from landscape attributes and/or species-specific dispersal capabilities (Calabrese and Fagan 2004). The most common connectivity indices reflect some measure of the predicted or actual frequency with which individuals move among patches, but connectivity can also be expressed as the number of links to other patches within a network (e.g., Rhodes et al. 2006).

Connectivity can be highly variable over space and time, ranging from the regular transition of nearly all individuals from one patch to another (i.e., seasonal migrations) to the total or near-complete isolation of individuals within a single patch (Bowne and Bowers 2004). When such movements occur, they can vary in timing, frequency, and distance according to interactions between intrinsic attributes of the individual (e.g., size, sex, age, motivation; Swingland and Greenwood 1983) and extrinsic attributes of the landscape (e.g., patch physiognomy, matrix resistance, resource quality gradients; Taylor et al. 1993, Ricketts 2001, Bowne et al. 2006). Without information on the frequency of such movements, the spatial and temporal scales over which they occur in a population, as well as factors driving inter-patch transitions, our perceptions of what constitutes the population and the processes that regulate it may be biased and misinformed, which can ultimately spawn inappropriate management strategies for conservation.

Biotic wetland connectivity pertains to the functional relationship among wetlands that arises via the movement of organisms (Haig et al. 1998). Determining the degree to which the biota of distinct wetlands interact with one another and the spatial scales over which these

interactions occur is a fundamental issue for wetland monitoring and conservation programs to consider (Trenham et al. 2001, Petranka et al. 2004, Roe and Georges 2007). Wetlands do not have to be physically connected by water flows for their biota to move between them, though the patchy occurrence of "isolated" wetlands within a terrestrial matrix superficially imposes a spatially structured distribution of discrete subpopulations connected only by occasional dispersal (Gibbs 2000, Gibbons 2003, Semlitsch and Bodie 2003). In this scenario, we can assume population regulation depends mostly on the quality of the focal wetland and adjacent terrestrial landscape, while the regional stability of a group of populations (i.e., a metapopulation; Harrison 1991) may hinge upon these occasional dispersal events (Marsh and Trenham 2001). However, when movements among wetlands allow individuals to exploit spatially distinct but critical resource patches, single wetlands should not be considered as harboring independent populations, as the processes that regulate them would ultimately depend upon both the focal wetland and other bodies of water throughout the landscape. Source–sink dynamics (Pulliam 1988) and habitat complementation (Dunning et al. 1992) are examples of processes where inter-patch movements strongly influence both local and regional population dynamics in wetland systems (Gill 1978, Pope et al. 2000).

Freshwater turtles are a group threatened by wetland loss and degradation (Burke et al. 2000), yet these threats often extend beyond the delineated wetland boundaries when turtles undertake essential terrestrial behaviors (Marchand and Litvaitis 2004, Steen and Gibbs 2004). Terrestrial movement across the landscape is arguably one of the least well understood aspects of turtle behavior, yet such information is critical for identifying and mitigating threatening processes. Due to logistical constraints, most studies of turtle movements are limited in their ability to describe the flows of animals across a large area and over extended time frames, both of which are important for addressing landscape-level questions in long-lived animals such as turtles. Consequently, the details of terrestrial inter-patch movements, such as the spatial scales over which they occur, their timing, rates, functional significance, and factors influencing their subsequent destination location are typically unknown, yet this information may be just as important as other biological characteristics (e.g., life history traits, demographics, habitat associations) upon which management plans are traditionally based.

We undertook an intensive capture–mark–recapture study of the eastern long-necked turtle (*Chelodina longicollis*) in a wetland network in southeastern Australia over a period that spanned a drought and the subsequent return of wet conditions. We assessed several measures of inter-wetland connectivity by documenting movements of marked individuals and compared these to some structural landscape metrics often used to predict connectivity. We also examined how inter-patch movements varied over space and time and among different age, sex, and size groups of turtles. We then compared the results from the capture–mark–recapture data to those collected at a drift fence intercepting turtles moving overland to assess the influence of sampling biases on our understanding of inter-patch movements. Together, our findings offer novel insights into both spatial and temporal dynamics of freshwater turtle populations as well as the sampling biases that can confound our understanding of these processes.

METHODS

Study site

Turtles were studied in Booderee National Park, a 7000-ha reserve located within the Commonwealth Territory of Jervis Bay in southeastern Australia (150°43′ E, 35°09′ S). Detailed descriptions of the study site are given by Kennett and Georges (1990), Norris et al. (1993) and Roe and Georges (2007, 2008). *Chelodina longicollis* is the only species of freshwater turtle occurring in the park, which is characterized by forested terrestrial habitats and a mosaic of freshwater dune lakes and a number of smaller wetlands ranging in size from 0.1 to 54 ha (Fig. 1). Wetlands were considered distinct only if they were isolated from each other by terrestrial habitat during their highest observed water levels. Though wetlands varied in hydroperiod along a continuous gradient (i.e., from permanently to infrequently flooded; Roe and Georges 2008), here we classify wetlands dichotomously as either permanent or temporary based on whether they dried at least once during our study, irrespective of longer-term flood–dry cycles.

Booderee is on a peninsula surrounded by the Tasman Sea and a brackish water lake (St. George's Basin) and inlet to the sea, with the nearest freshwater wetland on the mainland >5 km away and opposite the basin. Several areas of the park are moderately developed for the Australian Navy, residential housing, camping, and other visitor facilities. These facilities and the roads that connect them are generally not in the vicinity of study wetlands, though two moderately traveled roads bisect the westernmost wetland system (McKenzie-Windermere complex) from the easternmost wetland system (Blacks-Steamers complex). The region has a temperate maritime climate with a long-term average annual rainfall of ~1100–1200 mm (~80–100 mm per month), though the timing and intensity of rainfall can be highly variable (Roe and Georges 2008). Rainfall amounts were recorded daily at the Booderee ranger's depot, located within 5 km of all study wetlands.

Field data collection

We conducted a capture–mark–recapture study in 25 wetlands (14 temporary and 11 permanent), including all
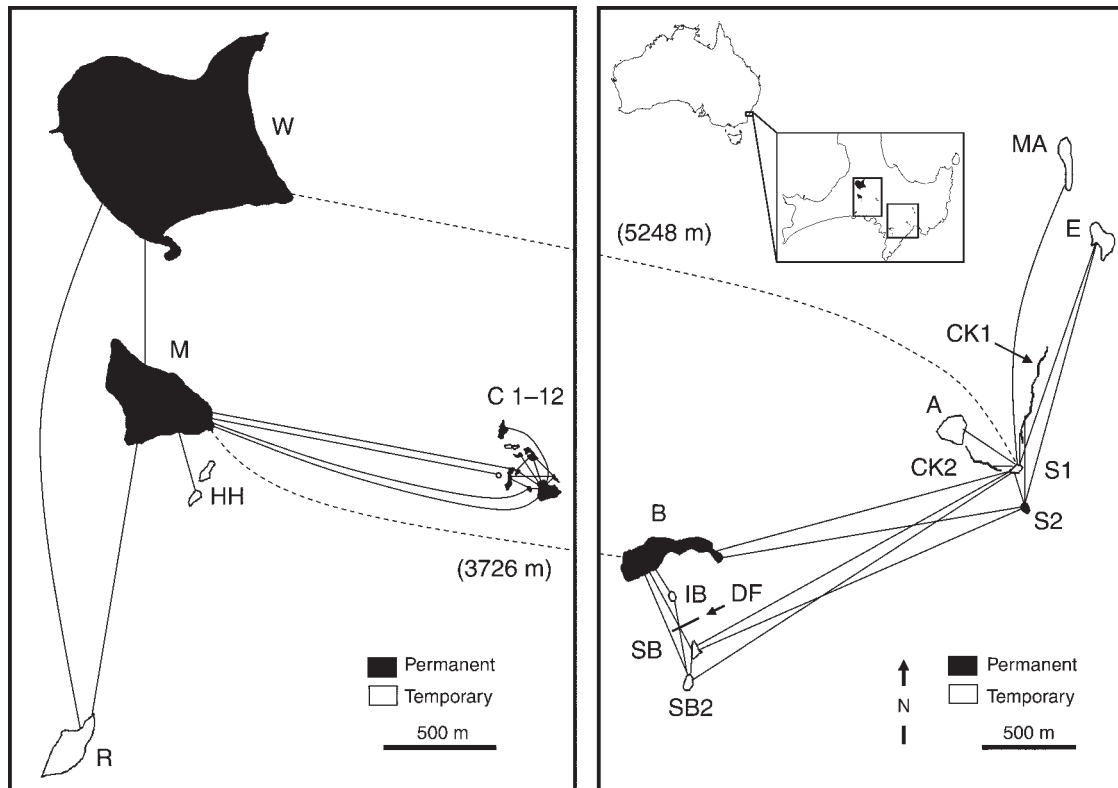
Fig. 1. Network of connections between wetlands in Booderee National Park, southeastern Australia, via turtle movements. The solid lines are movements detected during standardized sampling from 2004 to 2007, and the dashed lines are additional movements that were detected by examining the capture histories from the long-term data set (1983–2007). The inset at the top indicates the location of the study site, with the two boxed regions corresponding to the McKenzie-Windermere (westernmost box) and Blacks-Steamers (easternmost box) wetland systems. Wetland identifications are as follows: W, Lake Windermere; M, Lake McKenzie; HH, Halfway Holes; R, Ryan's Swamp; C, Claypits 1–12; B, Blacks Waterhole; IB, Inter-Blacks; SB, South Blacks; SB2, South Blacks 2; A, Alicia's Bog; S1, Steamers 1; S2, Steamers 2; E, Emily's Swamp; MA, Martha's Swamp; CK1, Northwest Steamers Creek; and CK2, North Steamers Creek. The location of the drift fence (DF) is also indicated.

wetlands that were identifiable from aerial photographs (Fig. 1). Wetlands were sampled for turtles using baited crab traps (80 × 60 × 25 cm, 3 cm mesh) and by hand. Hand capture techniques included snorkeling when wetlands were deep enough (water depth > 1 m), and wading, probing in vegetation, and netting in shallower wetlands until all accessible areas of the wetland had been covered. Samplings were divided into an equivalent spring (1 September–31 December) and summer (1 January–30 April) period in each of the three years of the study from 2004 to 2007, excluding periods of typical inactivity (May–August). During each sample period, wetlands were typically trapped for one to two days and subject to a similar number of hand-capture sessions, the exceptions being when a wetland was too shallow to set traps or was completely dry, and at the Claypits where only traps were used due to poor visibility and accessibility. Captures from the various sampling methods were combined into a single encounter session. This resulted in six capture–mark–recapture sessions (two in each of the three years) in which capture techniques were standardized as much as possible. In

addition to our standardized sampling regime, a small subset of the wetlands (M, W, R, and B; Fig. 1) had been sampled sporadically in twelve of the 21 years from 1983 to 2003 (Georges et al. 1986, Kennett and Georges 1990).

At each capture, we recorded the date, wetland of capture, and the turtle's identification code if previously marked. Unmarked turtles were marked with a unique code by notching the marginal scutes and underlying bone of the carapace. Straight-line carapace length (CL) and plastron length (PL) were measured to the nearest 0.1 mm using vernier calipers. All turtles with CL < 145 mm were classed as juveniles, and for those with CL > 145 mm, we were able to determine sex by examining the plastron curvature (see Kennett and Georges 1990). Minimum size at maturity in males is 145 mm, and in females 165 mm (Kennett and Georges 1990). All males >145 mm and only females >165 mm were classified as adults, while females between 145.0 and 164.9 mm were classed as subadults. Turtles were released at their capture locations within 24 hours.

We also captured turtles using a terrestrial drift fence and pitfall array constructed perpendicular to the axis of travel along a known turtle movement route (Fig. 1). The fence was constructed from polythene dampcourse (70 m long, 0.38 m high) buried several centimeters into the ground and held erect by wooden stakes. We buried seven sets of paired 20-L buckets, one on each side of the fence at 12-m intervals. Pitfalls were open from 6 September 2005 to 29 March 2006 and were checked once daily. Turtles were processed in the same manner as wetland captures, then released on the opposite side of the fence.

Data handling and analyses

At each of the recapture periods, turtles were classified first as either immature, male, or female (including subadult and adult individuals) and then according to whether they had moved between wetlands since their most recent capture in any of the previous sample periods. To determine if the proportion of turtles moving varied over time or between age or sex class groups, we used logistic regression (PROC LOGISTIC Model; SAS Institute 1999), with capture period and group as categorical factors in the model. To determine whether distance moved between wetlands differed among these three groups, we used a Kruskal-Wallis test (SPSS 1999). We then examined whether turtle size influenced distance traveled by regressing distance against plastron length.

We assessed several measures of actual and structural connectivity for each wetland. Structural connectivity measures included wetland size and two indices of wetland density. Wetland density was measured as the number of wetlands within a 2-km buffer of each wetland, and as the mean distance from the focal wetland to all others within the buffer. No structural features of the terrestrial matrix were examined due to the similarity of habitat between wetlands. Inter-wetland distance and wetland sizes (surface area) were measured using the Nearest Features and X-Tools extensions for ArcView GIS (ESRI 1992).

Our first measure of actual connectivity was determined by counting the number of connections with other wetlands via the movement of turtles; we refer to this connectivity metric as network connectivity hereafter. We then examined the relationship between network connectivity (response variable) and the three measures of structural connectivity (predictor variables) using Poisson regression (PROC GENMOD; SAS Institute 1999). We also examined whether permanent and temporary wetlands differed in their network connectivity using a Kruskal-Wallis test.

For our second measure of actual connectivity, we assessed the relative proportion of the total immigrant pool that a wetland received during each sampling period according to the following equation adopted from Bowne et al. (2006):

$$C_i = n_{ij}/(n_{total} - n_{ei})$$

where n_{ij} is the number of turtles moving into wetland i from all source wetlands j, n_{total} is the number of turtles that moved between wetlands across the entire site (i.e., the immigrant pool), and n_{ei} is the number of emigrants from wetland i. We refer to this connectivity metric as relative connectivity hereafter. In the above calculation, we subtracted emigrants from the total immigrant pool on a wetland specific basis because emigrants from a wetland cannot also be immigrants to the same wetland in a capture period. Because each wetland has a different denominator in this calculation, proportions do not sum to one, but instead ranged from 1.04 to 1.09. Next, we examined whether permanent and temporary wetlands differed in the number of immigrants received during each sampling period using chi-square tests, with the null hypothesis assuming equal immigration for the two wetland types. For each wetland type and sampling period combination, we also assessed whether individual wetlands differed in immigrant numbers using chi-square tests, again with the null hypothesis that immigration would be equal among wetlands. We realize that even if movements were random, the different size and spatial arrangements of wetlands in the landscape would likely lead to the rejection of the null hypothesis. However, we elected not to construct a null hypothesis of expected movements based in some way on these attributes, as this would be tantamount to predicting connectivity from structural landscape variables alone, whereas we were interested in comparing actual connectivity (Calabrese and Fagan 2004). Instead, we assessed the relationship between relative connectivity and $\log_{10}$-transformed values for the three structural measures of connectivity (density metrics and size) using multiple regression.

For our third measure of connectivity, we assessed transition probabilities (ψ) between wetland pairs after accounting for survival (Φ) and capture (p) probabilities using the program MARK version 4.2 (White and Burnham 1999). This measure of connectivity is referred to as transition or movement probability hereafter. As a first step in the analysis, we constructed capture histories for the McKenzie-Windermere and Blacks-Steamers wetland systems separately (due to the infrequency of movements between them, see *Results* and Fig. 1) and examined whether survival and capture probabilities varied over time or according to maturity status. We used a fully saturated model with time dependence for two groups (adult and juvenile) and then fitted a series of reduced-parameter models. Turtles that were removed from the population (trap deaths, subjects of manipulative studies) were accounted for as a negative number in the capture histories (Cooch and White 2004). Guided by the most well-supported models for survival and capture probabilities, we then constructed candidate model sets examining transition probabilities using multistate models (Arnason 1973, Brownie et al. 1993). Multistate models were limited to a core set of wetlands where the majority of captures took place and

TABLE 1. Percentage of recaptured turtles that moved between wetlands in Booderee National Park, southeastern Australia, over the five capture intervals from 2004 to 2007.

Group	Capture period				
	Spr 2004–Sum 2005	Sum–Spr 2005	Spr 2005–Sum 2006	Sum–Spr 2006	Spr 2006–Sum 2007
Male	44.2	30.5	33.8	28.1	22.0
Female	36.4	22.8	29.5	29.6	27.4
Juvenile	13.6	18.7	9.6	22.6	15.8

Notes: Values are percentages of turtles that were captured in a wetland different from their most recent previous capture in any of the prior sampling periods. Percentages are not corrected for survival or encounter probability.

where sampling protocols were standardized as much as possible. These included B, SB, SB2, S1, and S2 in the Blacks-Steamers system and W, M, and R in the McKenzie-Windermere system.

Our first multistate model tested whether adults differed from juveniles in transition probability by holding transition probability constant both over time and among wetlands, but allowing for differences between maturity groups. Next, we tested whether transition probabilities differed on a temporal and wetland-specific basis for adults only, as such detailed models failed to converge for juveniles. Model selection was based on the information theoretical approach (Akaike Information Criterion), with the most supported models having the lowest values. When multistate models were overparameterized, movement probabilities that could not be estimated were fixed to zero to achieve model convergence (e.g., Spendelow et al. 1995). The most saturated model in a candidate model set was tested for its adequacy to describe the data using a goodness-of-fit (GOF) test. In the initial survival and capture analyses, GOF was tested using the bootstrap procedure with 500 simulations, and an overdispersion parameter, $\hat{c}$, was derived by dividing the model deviance by the mean of simulated deviances (Cooch and White 2004). In the multistate models, GOF was tested in the program U-CARE (Pradel et al. 2003), and $\hat{c}$ derived by dividing the χ^2 statistic by the degrees of freedom (Cooch and White 2004). Where there was evidence for overdispersion ($1 < \hat{c} < 3$; Cooch and White 2004), we adjusted models with the derived $\hat{c}$ to improve model fit and calculate a quasi-likelihood estimator, $QAIC_c$ (Burnham and Anderson 1998). We used model averaging in reporting all parameter estimates to account for model uncertainty.

To examine whether movement probabilities declined with increasing distance between wetland pairs, we ran Mantel tests for each sampling period using PopTools (Hood 2008). When there were two movement probabilities between the same wetland pair (i.e., when each received some immigrants from the other), we used the higher of the two probabilities. We then averaged the movement probabilities over all sample periods for each wetland pair and used these values to estimate the relationship between movement probability and inter-wetland distance with a negative exponential regression model.

To assess whether our capture techniques that focused on wetlands only (traps and snorkeling) yielded a demographically biased sample of turtles that moved between wetlands, we compared demographic aspects of turtles captured in wetlands to those captured moving overland at the drift fence. Comparisons were limited to those captured in the wetlands near the drift fence (B, IB, SB, and SB2). A series of chi-square tests were run using the PROC FREQ procedure in SAS (1999) to examine potential differences in the size–frequency distributions among three groups: (1) all turtles captured in the wetlands during the capture–mark–recapture sampling, (2) only turtles detected moving overland at the drift fence, and (3) only turtles detected to have moved overland between wetlands by examining their wetland capture–recapture histories (i.e., a subset of the entire wetland sample). Significance values for this series of comparisons were lowered to $\alpha < 0.016$ using the Dunn-Sidak correction.

RESULTS

We recorded a total of 4250 captures of 2580 individuals (703 M, 907 F, 970 J) from 2004 to 2007. Of the 1057 turtles (331 M, 436 F, 290 J) that were recaptured, 33% (39% M, 37% F, 19% J) moved between wetlands at least once. The proportion moving varied between periods and sex/ontogenetic groups (period, $\chi^2 = 7.8$, df = 1, $P = 0.005$, group, $\chi^2 = 14.1$, df = 1, $P < 0.001$; Table 1). Turtles moved between wetlands separated by 16–1946 m, with larger turtles moving longer distances, though this relationship was only weak ($r^2 = 0.03$, $P < 0.001$; Fig. 2). Distance moved overland between wetlands was highest in males (700 ± 39 m, mean ± SE), intermediate in females (589 ± 32 m), and lowest in juveniles (412 ± 49 m; Kruskal-Wallis $\chi^2 = 14.08$, df = 2, $P = 0.001$).

Every wetland was connected to at least one other via turtle movements (Fig. 1), though permanent wetlands had a larger number of connections (3.8 ± 0.6) than temporary wetlands (2.3 ± 0.6; Kruskal-Wallis $\chi^2 = 4.35$, df = 1, $P = 0.037$; Fig. 3). However, no measure of structural connectivity explained actual network connectivity ($P \geq 0.771$ in all cases). In examining the network of connections, we identified two wetland systems within which movements between wetlands were common, hereafter referred to as the McKenzie-Windermere and Blacks-Steamers systems (Fig. 1).
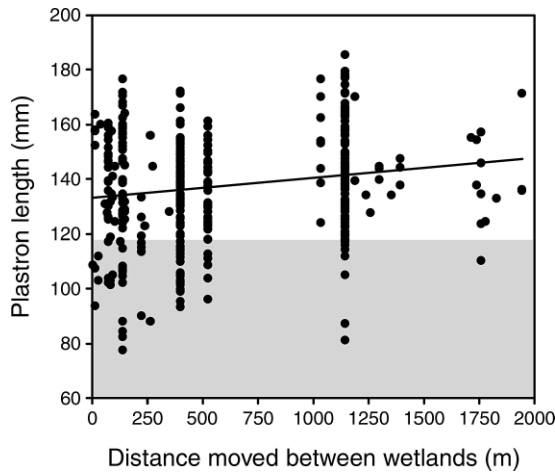
FIG. 2. Relationship between turtle size and overland distance moved between wetlands for 442 movements. The unshaded region denotes adult males and both subadult and adult females, while the shaded area indicates immature individuals.

Polygons that encompassed all connected wetlands within each system were 460 and 290 ha. Only two adult males were known to have moved between these systems (one in each direction), traveling distances of 5248 and 3726 m. Both were determined to have moved only by examining the long-term capture–recapture data set, with times between captures spanning 1985 to 2007 (22 years) and 1996 to 2005 (9 years).

Wetlands were not equal recipients of immigrants over time (Fig. 4), but no measures of structural connectivity accounted for any of this variance in relative connectivity ($r^2 = 0.22$, $P = 0.659$). Relative connectivity was highest in permanent wetlands from
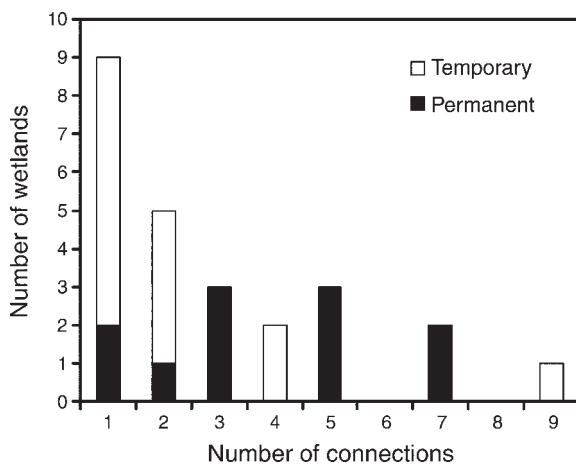

FIG. 3. Number of connections with other wetlands (network connectivity) via the movement of turtles (bars) for 14 temporary and 11 permanent wetlands in Booderee National Park from 2004 to 2007. Note that no measure of structural connectivity explained variance in network connectivity (see *Results*).
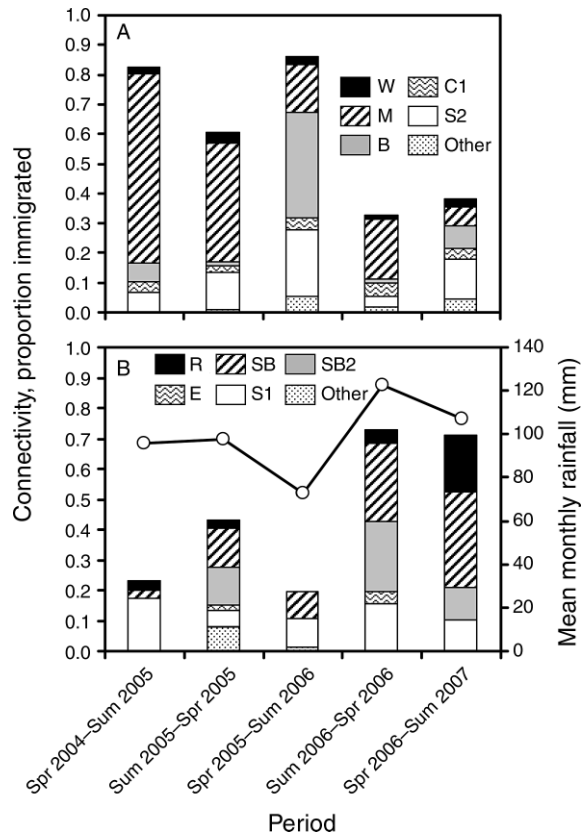

FIG. 4. Relative proportion of immigrant turtles (bars) entering (A) permanent and (B) temporary wetlands during the five sampling intervals between 2004 and 2007 (Spr, spring [1 September–31 December]; Sum, summer [1 January–30 April]), excluding periods of typical inactivity (May–August). Rainfall (open circles and solid lines) is also shown in (B). Wetlands are arranged in order of decreasing size from top to bottom within each bar. Note that the keys for wetland identification are different on the two graphs. See Fig. 1 for full wetland identifications.

spring 2004 to summer 2006 ($\chi^2 \geq 17.1$, df = 1, $P < 0.001$ in all cases), but highest in temporary wetlands from summer 2006 to summer 2007 ($\chi^2 \geq 12.3$, df = 1, $P < 0.001$ in both cases). Immigrant numbers were not equally distributed among the permanent wetlands from spring 2004 to spring 2006 ($\chi^2 \geq 35.3$, df = 4, $P < 0.001$ in all cases), while individual temporary wetlands differed in relative immigration from summer 2006 to summer 2007 ($\chi^2 \geq 26.7$, df = 4, $P < 0.001$ in both cases). The relative connectivity of temporary wetlands increased with the mean monthly rainfall amount during the capture interval ($r^2 = 0.83$, $P = 0.033$; Fig. 4).

In the Blacks-Steamers system, the model with the most support in the initial survival and capture analyses was for constant and equal survival between adults and juveniles, but where capture probability varied according to maturity status (Table 2). Juvenile survivorship was 0.93 ± 0.04 and capture probability ranged from 0.14 to 0.22, while adult survivorship was 0.94 ± 0.02

TABLE 2. Model selection for factors influencing survival (Φ), capture (p), and movement (ψ) probabilities for turtles in the Blacks-Steamers (B-S) and McKenzie-Windermere (M-W) wetland systems.

Site	Model†	QAIC$_c$	ΔQAIC$_c$	Model weight	k (no. parameters)	Deviance
Survivorship models (adults and juveniles)						
B-S	$\Phi(\cdot)p(g)$	2085.62	0.000	0.382	3	115.01
	$\Phi(\cdot)p(g{\times}t)$	2086.25	0.627	0.279	11	99.44
	$\Phi(g)p(g)$	2087.49	1.864	0.150	4	114.90
	$\Phi(g)p(g{\times}t)$	2087.91	2.286	0.122	12	99.05
M-W	$\Phi(\cdot)p(g{\times}t)$	1758.89	0.000	0.439	11	96.54
	$\Phi(g)p(g{\times}t)$	1759.99	1.101	0.254	12	95.62
	$\Phi(g)p(t)$	1760.53	1.645	0.193	7	106.27
	$\Phi(\cdot)p(t)$	1762.36	3.471	0.078	6	110.11
Multistate models (adults and juveniles)						
B-S	$\Phi(\cdot)p(w{\times}g)\psi(g)$	3459.51	0.000	0.999	11	1373.99
	$\Phi(\cdot)p(w{\times}g)\psi(\cdot)$	3477.17	17.67	0.001	10	1393.70
M-W	$\Phi(\cdot)p(w{\times}g)\psi(g)$	3020.60	0.000	0.945	9	645.25
	$\Phi(\cdot)p(w{\times}g)\psi(\cdot)$	3026.29	5.694	0.055	8	652.97
Multistate models (adults only)						
B-S	$\Phi(w)p(w)\psi(w{\times}t)$	2089.03	0.000	0.737	32	570.90
	$\Phi(\cdot)p(w)\psi(w{\times}t)$	2091.09	2.062	0.263	29	579.60
M-W	$\Phi(\cdot)p(w{\times}t)\psi(w{\times}t)$	2187.34	0.000	0.923	32	251.66
	$\Phi(w)p(t)\psi(w{\times}t)$	2192.78	5.438	0.061	23	275.77

Notes: Time (t) indicates sample interval, group (g) separates adult from juvenile, and wetland (w) designates the different strata.

† The overdispersion parameter, $\hat{c}$, in the survivorship models was 1.15 ($P = 0.154$) and 2.49 ($P < 0.001$) in the B-S and M-W systems, respectively. In the multistate models, $\hat{c}$ was 0.81 ($\chi^2 = 73.71$, $P = 0.907$) and 1.77 ($\chi^2 = 118.79$, $P < 0.001$) in the B-S and M-W systems, respectively.

and capture probability ranged from 0.40 to 0.42. In the McKenzie-Windermere system, the best fit model was for constant and equal survival between adults and juveniles, and both group and time dependence in capture probability (Table 2). Juvenile survivorship was 0.86 ± 0.07 and capture probability ranged from

0.13 to 0.30, while adult survivorship was 0.85 ± 0.03 and capture probability ranged from 0.18 to 0.43.

Multistate models indicated that transition probability differed according to maturity status, with adult and juvenile transition probabilities in the Blacks-Steamers system of 0.10 ± 0.01 and 0.04 ± 0.01, respectively, and

TABLE 3. Movement probabilities (±SE) of adult turtles between wetland pairs in the Blacks-Steamers wetland system.

Origin wetland (j)			Destination wetland (i)			
	Period	n	S1 (T)	S2 (P)	B (P)	SB (T)
S1 (T)	spr 2004–sum 2005	12	**0.67**	0.33 ± 0.14	0.00	0.00
	sum–spr 2005	23	**0.42**	0.47 ± 0.11	0.00	0.11 ± 0.05
	spr 2005–sum 2006	21	**0.47**	0.43 ± 0.17	3:21	0.10 ± 0.08
	sum–spr 2006	12	**11:12**	1:12	0.00	0.00
	spr 2006–sum 2007	18	**0.63**	0.37 ± 0.11	0.00	0.00
S2 (P)	spr 2004–sum 2005	17	0.52 ± 0.13	**0.48**	0.00	0.00
	sum–spr 2005	11	0.24 ± 0.13	**0.76**	0.00	0.00
	spr 2005–sum 2006	19	2:19	**17:19**	0.00	0.00
	sum–spr 2006	29	0.38 ± 0.09	**0.62**	0.00	0.00
	spr 2006–sum 2007	28	4:28	**24:28**	0.00	0.00
B (P)	spr 2004–sum 2005	28	0.02 ± 0.02	0.01 ± 0.01	**0.88**	0.09 ± 0.06
	sum–spr 2005	39	0.00	0.00	**0.37**	0.63 ± 0.09
	spr 2005–sum 2006	28	0.00	0.00	**0.92**	0.08 ± 0.08
	sum–spr 2006	39	0.00	0.00	**0.13**	0.87 ± 0.06
	spr 2006–sum 2007	25	1:25	0.00	**0.58**	0.42 ± 0.29
SB (T)	spr 2004–sum 2005	4	0.00	0.00	0.41 ± 0.23	**0.56**
	sum–spr 2005	4	0.00	0.00	0.24 ± 0.22	**0.76**
	spr 2005–sum 2006	26	0.01 ± 0.01	0.01 ± 0.01	0.82 ± 0.07	**0.16**
	sum–spr 2006	9	0.00	0.00	0.28 ± 0.24	**0.72**
	spr 2006–sum 2007	29	0.02 ± 0.02	0.00	0.16 ± 0.06	**0.82**

Notes: Wetlands are classified as either temporary (T) or permanent (P), and n is the number of turtles recaptured from the wetland of origin in each sampling period. Ratios are reported for parameters fixed to zero to achieve model convergence, but where movement was known to have occurred. Probability of remaining within a wetland (boldface) is 1.00 minus the sum of movement probabilities to other wetlands. Wetlands where captures were too few or inconsistent were not included in the model (IB, AB, EM, MA, CK1, CK2). Owing to their close proximity, SB and SB2 were grouped together to increase sample sizes.

TABLE 4. Movement probabilities (±SE) of adult turtles between wetland pairs in the McKenzie- Windermere wetland system.

Origin wetland (j)			Destination wetland (i)		
	Period	n	W (P)	M (P)	R (T)
W (P)	spr 2004–sum 2005	19	**1.00**	0.00	0.00
	sum–spr 2005	62	**0.94**	0.06 ± 0.03	0.00
	spr 2005–sum 2006	37	**0.95**	0.05 ± 0.04	0.00
	sum–spr 2006	68	**0.87**	0.11 ± 0.06	0.02 ± 0.03
	spr 2006–sum 2007	71	**0.99**	0.01 ± 0.03	0.00
M (P)	spr 2004–sum 2005	33	0.00	**0.97**	0.03 ± 0.05
	sum–spr 2005	101	0.01 ± 0.01	**0.98**	0.01 ± 0.02
	spr 2005–sum 2006	53	0.02 ± 0.02	**0.98**	0.00
	sum–spr 2006	60	0.01 ± 0.01	**0.92**	0.07 ± 0.07
	spr 2006–sum 2007	66	< 0.01 ± < 0.01	**0.40**	0.60 ± 0.67
R (T)	spr 2004–sum 2005	51	0.02 ± 0.02	0.75 ± 0.10	**0.23**
	sum–spr 2005	41	0.00	0.40 ± 0.37	**0.60**
	spr 2005–sum 2006	11	0.00	0.14 ± 0.19	**0.86**
	sum–spr 2006	4	0.00	2:4	**2:4**
	spr 2006–sum 2007	4	0.00	1:4	**3:4**

Notes: Wetlands are classified as either temporary (T) or permanent (P), and n is the number of turtles recaptured from the wetland of origin in each sampling period. Ratios are reported for parameters fixed to zero to achieve model convergence, but where movement was known to have occurred. Probability of remaining within a wetland (boldface) is 1.00 minus the sum of movement probabilities to other wetlands. The Claypits and HH were not included in the models due to less consistent sampling and few captures, respectively.

0.09 ± 0.01 and 0.04 ± 0.01 in the McKenzie-Windermere system (Table 2). Multistate models also indicated both wetland- and time-dependent variation in adult transition probability in each wetland system (Tables 2, 3, and 4). Transition probability declined with increasing distance between wetland pairs in each sampling period ($r = -0.56$ to -0.64, $P \leq 0.019$; Fig. 5). We note here that our estimates of ψ, Φ, and p are not annual probabilities, but instead reflect probabilities over our biannual sampling intervals.

The proportions of immature turtles from the drift fence and wetland samples were 45% and 42%, respectively, and size–frequency distributions did not differ between these groups ($\chi^2 = 11.1$, df = 16, $P = 0.803$; Fig. 6A). In contrast, only 15% of turtles detected to have moved between wetlands by examining capture–recapture histories from wetland captures were immature, and the size–frequency distribution of this group was biased toward larger turtles compared to both the entire wetland and drift fence samples ($\chi^2 \geq 50.4$, df = 16, $P < 0.001$ in both cases; Fig. 6B).

DISCUSSION

The movement models and analyses described in this paper represent one of the most detailed studies of wetland connectivity for any freshwater reptile. Our study is unique in that we were able to sample all wetlands within a system that was, to the best of our knowledge, isolated from other turtle populations. This allowed us to estimate movement rates with associated variance, together with knowledge of the source, destination, and timing of movements across a large area. The most important findings relevant to freshwater turtle population dynamics and management of wetland systems were that (1) individual wetlands should not be

considered the minimum habitat units harboring demographically distinct subpopulations, (2) the probability of inter-patch movement decreased with increasing distance between wetlands, (3) understanding motivations for movement provided much insight into the spatial and temporal dynamics of populations, and (4) sampling methods can bias our understanding of connectivity for some demographic groups.

Our findings contest the conventional conception that individual wetlands harbor independent demographic subpopulations of freshwater turtles connected only via occasional dispersal. We estimate that 33% of turtles transitioned between wetlands, but after scaling this movement rate to the number of generations elapsed during our study (time to maturity 8–12 yr; Chessman 1978) inter-wetland movement rates exceed 88% per generation (calculated as in Bowne and Bowers 2004). This rate is among the highest recorded in a recent literature review of inter-patch movements (Bowne and Bowers 2004), and illustrates that most turtles in our study system will associate with more than one wetland over a period of several years. Consequently, we agree with several recent studies of aquatic and semiaquatic vertebrates that suggest groups of wetlands should be considered the minimum habitat units harboring local populations (Haig et al. 1998, Joyal et al. 2001, Petranka et al. 2004, Roe and Georges 2007).

In this more complex model of spatial population structure where a single population is spread over groups of wetlands, inter-patch movements were not so frequent or widespread such that all wetlands within the landscape were connected equally. Inter-wetland distance was a strong predictor of transition probability, with probability declining as distance increased (Fig. 5). Movements are typically spatially limited in animal
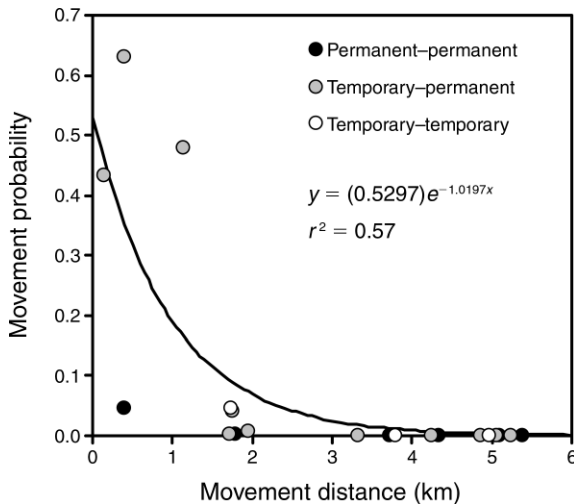
FIG. 5. Relationship between movement probability and distance for adult *Chelodina longicollis* traveling among a subset of wetlands (S1, S2, B, SB, M, W, R). Movement probabilities are not annual rates, but instead reflect movement between spring (September–December) and summer (January–April) sampling periods. We fit a negative exponential curve to estimate the relationship between these variables (e.g., Berven and Grudzien 1990, Trenham et al. 2001).

populations (Berven and Grudzein 1990, Kot et al. 1996, Trenham et al. 2001), though the distance where movements are assumed to grade from intrapopulational to interpopulational varies. We observed a relatively high degree of connectivity among wetlands separated by up to 1.2 km (e.g., Lake McKenzie and Ryan's Swamp; Figs. 1 and 5). However, not all measures of structural landscape connectivity were good predictors of actual connectivity. Neither network nor relative connectivity was related to any physical landscape attribute commonly used as a surrogate for actual connectivity (e.g., patch density, inter-patch distance, and patch size; Moilanen and Nieminen 2002, Calabrese and Fagan 2004). It should be noted that our wetland system was not bisected by heavily traveled road networks, agriculture, or other potential barriers known to compromise movements and population dynamics in turtles elsewhere (Marchand and Litvaitis 2004, Steen and Gibbs 2004, Bowne et al. 2006).

Though the overall influence of inter-wetland distance on transition probability was strong, several lines of evidence indicate that connectivity was influenced by the context of movements as well. Movement probabilities between permanent and temporary wetlands were regularly higher than 30% and as high as 87%, even between distant wetlands (e.g., 1.2 km from Lake McKenzie to Ryan's Swamp), whereas transitions between wetlands of the same hydroperiod classification never exceeded 11% even when in close proximity to one another (e.g., 0.4 km between Lakes Windermere and McKenzie; Tables 3 and 4, Fig. 5). Both the magnitude and direction of movements were highest into perma-

nent wetlands in periods of drought, but this trend reversed when rainfall increased and temporary wetlands flooded (Fig. 4). Additionally, network connectivity was higher in permanent lakes than temporary wetlands (Fig. 3). Interpreting such temporal dynamics of movement in the context of habitat selection behavior provides useful insight into these connectivity patterns. During drought, the few permanent wetlands that retain water serve as relatively stable aquatic refuges where turtles have a higher probability of survival (Roe and Georges 2008), but during periods of heavy rainfall, temporary wetlands offer high-quality foraging resources that allow turtles to grow faster and increase reproductive output (Georges et al. 1986, Kennett and Georges 1990). Two-way movements of the magnitude and frequency observed in this study imply intrapopulational migration between critical resource patches rather than interpopulational dispersal. This distinction is not trivial, as it has fundamental implications for our understanding of both the mechanistic basis of movement and its influence on population dynamics and management (Semlitsch 2008). We propose that the high degree of connectivity between temporary and permanent wetlands reflects the strong but shifting resource quality gradients that drive movements between them, and contend that habitat selection and motivation to move should be considered in connectivity assessments (Bélisle 2005, Bowne et al. 2006).

The spatial extent over which individuals perceive the landscape and their motivations to move often differ according to sex and ontogeny in turtles (Morreale et al. 1984, Gibbons et al. 1990, Scribner et al. 1993, Bowne et al. 2006). It follows that connectivity should also vary among these groups, though we found contradictory evidence that this was the case in our system. For instance, body size had little influence of biological importance on movement distances between wetlands (Fig. 2), though adult males did move the longest distances of any group. The more puzzling discrepancy in our data comes from our comparison of juvenile and adult movement rates. Inter-wetland movement rates and size–frequency distributions derived from our aquatic sampling protocols strongly suggest that immature and smaller turtles move less frequently than adults (Table 1, Fig. 6B), even after accounting for the considerable ontogenetic differences in capture probabilities (Table 2). However, these trends were not evident in the terrestrial drift fence method of sampling overland movements (Fig. 6A). We cannot easily explain how these two sampling techniques could account for such a difference in our perception of the influence of ontogeny on movement. One possibility is that the drift fence captures all turtles that attempt to move overland, whereas the wetland sampling captures only those that are successful in completing the movement. This explanation is plausible only if juveniles incur higher mortality than adults when moving overland, or if they are less likely to find another wetland after dispersing.
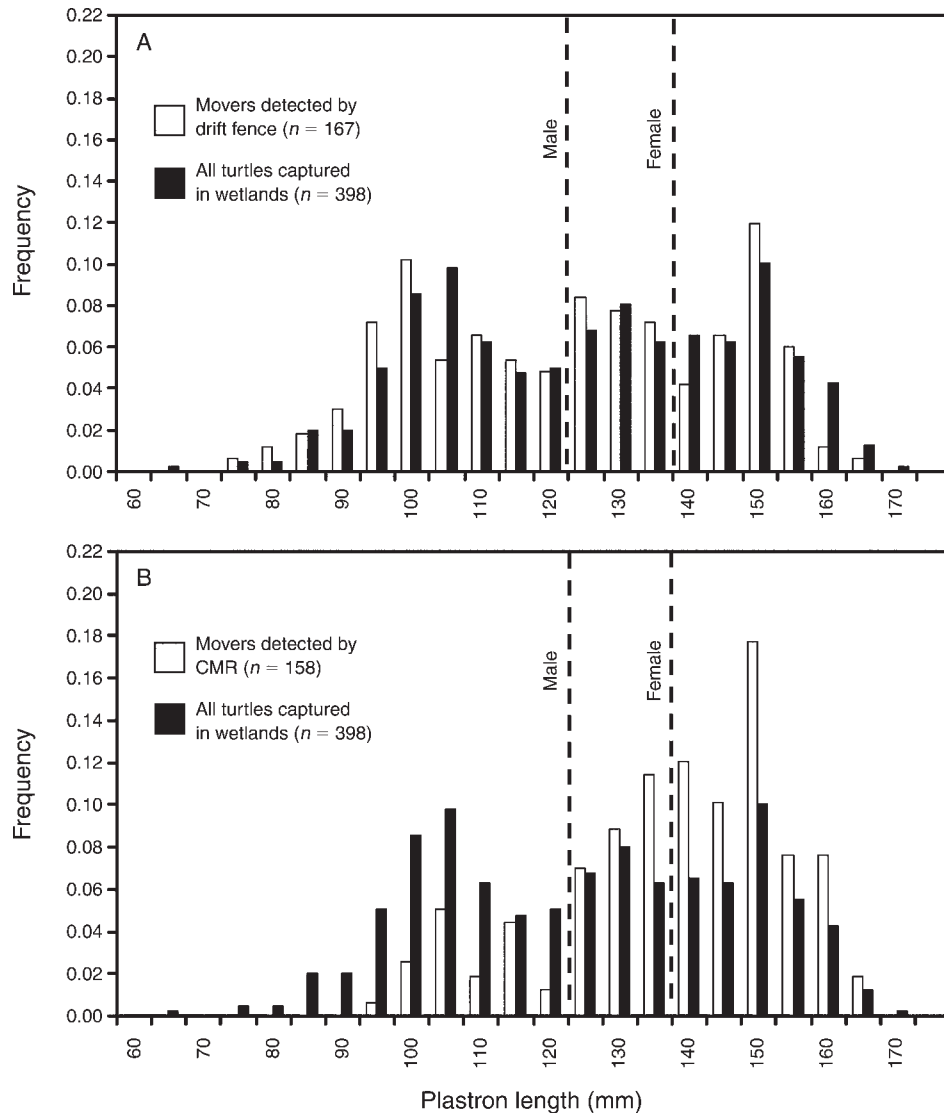
FIG. 6.   Size–frequency distributions of all turtles captured in wetlands (black bars) compared to (A) those that were detected moving overland between wetlands during the drift fence sampling, and (B) those that were detected to have moved overland between wetlands by examining capture–mark–recapture (CMR) histories of encounters during standard wetland sampling protocols (trapping and snorkeling). The sizes at which males and females mature are indicated by the vertical dashed lines. Only wetlands sampled near the drift fence were included in this analysis (B, IB, SB, SB2).

However, general mortality rates (which include mortality and the "disappearance" of dispersers from the study system in our models) did not differ ontogenetically. It is also possible that the drift fence is somehow biased toward capturing juveniles. Whatever the cause of the discrepancy, the drift fence encounters suggest that small and immature turtles may not be as limited in their ability to move between wetlands as was previously thought. For instance, use of the terrestrial drift fence reduced the minimum size at which turtles in the area were known to undertake inter-patch movements by >20 mm PL (24 mm CL), which is the equivalent of a 2–3 year age difference (estimated from growth rates of 9–10 mm/yr CL; J. H. Roe, *unpublished data*). We caution

that sample biases in capture techniques may lead to misconceptions of inter-wetland connectivity in freshwater turtles.

Even though our long-term sampling was not conducted with the same rigor as our intensive three-year study, one notable insight on dispersal capabilities can be taken from this more extended sampling. The longest dispersal from 2004 to 2007 was ~2 km, but by examining capture–recapture histories spanning back >20 years to 1983, we detected dispersal events nearly three times as far that linked the two wetland systems. This finding influences our perception of the distances over which gene flow and population rescue can occur (Keister et al. 1982, Burke et al. 1995), and perhaps our

understanding of the spatial scales over which turtles can perceive their environment (Bowne and White 2004). Long-term studies are especially critical for identifying infrequent movements that have important implications for population and metapopulation dynamics, and the evolution of behavior in long-lived species such as turtles (Gibbons et al. 1990, Burke et al. 1995, Roe and Georges 2008).

CONCLUSIONS

Wetland complexes should represent the minimum habitat unit harboring a population of turtles at our site, though the specifics of how to delineate population boundaries should be context dependent. For instance, the movements of *C. longicollis* suggest the "patchy population" concept proposed by Harrison (1991) to be a suitable classification for how populations are structured in space, but we argue that the most important consideration in delineating a population is to consider the scale at which all requirements of the species in question are met. In our system, wetlands separated by up to 1.2 km and encompassing areas of several hundred hectares exchanged individuals in a manner consistent with migratory responses to spatio-temporal variation in resource quality within a population, but the declining frequency of movements beyond this distance suggests dispersal between distinct populations. Both the degree to which wetlands were connected and the spatial scales over which these connections extended were in large part products of temporally variable resource quality gradients and the spatial arrangements of permanent lakes and temporary wetlands in the landscape. The conditions at other locations may be very different, thus limiting the generalizations that we can make between species and systems.

Nevertheless, examining how connectivity varies across the landscape and over time in an area minimally impacted by human development can provide an important reference for comparisons to more heavily modified areas. In terms of setting a baseline for other studies, perhaps our most important contribution is that inter-wetland connectivity was highly variable over space and time. Both the frequencies and directions of movement between the same wetland pairs varied considerably over time, not according to changes in the matrix though which turtles were traveling, but presumably in response to changes in intra-patch quality and associated fitness consequences in permanent and temporary wetlands (sensu Fretwell 1972, Spendelow et al. 1995). Thus, just as structural connectivity can have little bearing on the actual movements of animals (Tischendorf and Fahrig 2000, Calabrese and Fagan 2004), measures of actual connectivity may not reflect the degree to which different landscapes impede or facilitate movements unless motivation to move is first understood and then standardized (Bélisle 2005). To this end, we suggest that some understanding of spatial and temporal variation in intra-patch processes (e.g., quality

and extent) and the expected movement responses of animals (e.g., habitat selection) over long time frames would greatly advance our understanding of landscape connectivity. In the same vein, we caution that even direct and detailed measures of actual connectivity can be sensitive to methodological biases for particular demographic groups, a finding that should be of concern to those researching any species with life stages that are inherently difficult to study.

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