

MAINTENANCE OF VARIABLE RESPONSES FOR COPING WITH WETLAND DRYING IN FRESHWATER TURTLES

JOHN H. ROE¹ AND ARTHUR GEORGES

Institute for Applied Ecology, University of Canberra, Canberra, Australian Capital Territory 2601 Australia

Abstract. Aquatic animals inhabiting temporary wetlands must respond to habitat drying either by estivating or moving to other wetlands. Using radiotelemetry and capture–mark–recapture, we examined factors influencing the decisions made by individuals in a population of freshwater turtles (*Chelodina longicollis*) in response to wetland drying in southeastern Australia. Turtles exhibited both behaviors, either remaining quiescent in terrestrial habitats for variable lengths of time (terrestrial estivation) or moving to other wetlands. Both the proportion of individuals that estivated terrestrially and the time individuals spent in terrestrial habitats increased with decreasing wetland hydroperiod and increasing distance to the nearest permanent wetland, suggesting behavioral decisions are conditional or state dependent (i.e., plastic) and influenced by local and landscape factors. Variation in the strategy or tactic chosen also increased with increasing isolation from other wetlands, suggesting that individuals differentially weigh the costs and benefits of residing terrestrially vs. those of long-distance movement; movement to other wetlands was the near universal strategy chosen when only a short distance must be traveled to permanent wetlands. The quality of temporary wetlands relative to permanent wetlands at our study site varies considerably and unpredictably with annual rainfall and with it the cost–benefit ratio of each strategy or tactic. Residency in or near temporary wetlands is more successful during wet periods due to production benefits, but movement to permanent wetlands is more successful, or least costly, during dry periods due to survival and body condition benefits. This shifting balance may maintain diversity in response of turtles to the spatial and temporal pattern in wetland quality if their response is in part genetically determined.

Key words: *Australia; behavior; Chelodina longicollis; estivation; freshwater turtle; partial migration; plasticity; population; temporary wetland; terrestrial habitat.*

INTRODUCTION

Organisms in landscapes characterized by spatial and temporal variability have evolved morphological, physiological, and behavioral life history traits that allow for both survival and production (growth and reproduction) despite stochastic fluctuations in habitat extent or patch quality. Movement among habitats or patches (i.e., migration) is one behavior used by several taxonomic groups in variable environments (Alerstam et al. 2003), but residency within the variable habitat or patch is also widespread, often requiring periodic estivation or dormant life stages (Christian et al. 1996, Cáceres and Tessier 2003). In many species, however, a decision to migrate or reside is not obligate, as variation in the behavioral response within a species or population can exist. Such a scenario has been described as a “facultative” or “partial” response (Terrill and Able 1988).

Several proximate and ultimate factors are thought to maintain variable responses within a population. Variable responses may exist between individuals that differ

in age, sex, body size, experience, or dominance position (Swingland 1983), or alternate responses may be frequency dependent, where the tactic chosen by an individual is based on the behavior of others (Lundberg 1987). In the previous scenarios, intraspecific competition during resource scarcity is thought to ultimately maintain the variation, but the average fitness payoffs of the strategies or tactics may or may not be equal (Dominey 1984). It is also possible that variation is due to genetic differences among individuals irrespective of other asymmetries (Pulido et al. 1996, Alerstam and Henderström 1998), or phenotypic plasticity, where behavioral or life history decisions are influenced by the individual’s environment or physiological state (Semlitsch et al. 1990, Houston and McNamara 1992). Questions pertaining to variable responses in fluctuating environments, specifically whether to move between patches or remain and cope with environmental extremes, have been examined primarily in species with well-known, long, or conspicuous migrations (e.g., birds, insects, large mammals), but the same or other factors are likely at work in shaping the responses of animals using landscapes on smaller spatial scales, where habitats are also patchy and temporally variable.

Freshwater wetland systems can be highly variable environments. Wetlands are patchy in space, and the

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¹ E-mail: roe@aerg.canberra.edu.au

environment can differ widely among different wetlands or within a given wetland over time (Euliss et al. 2004), especially in temporary wetlands (i.e., wetlands that periodically dry; Kennett and Georges 1990, Bauder 2005). Consequently, the opportunity to move between wetlands and the associated costs vary both spatially and temporally. Animals from diverse taxonomic groups eventually face the common challenge of wetland drying by either residing or moving to other wetlands, and both strategies or tactics typically exist within many groups (e.g., amphibians [Denoël et al. 2005], fish [Sayer and Davenport 1991], invertebrates [Cáceres and Tessier 2003, Hall et al. 2004], reptiles [Gibbons et al. 1983, Christiansen and Bickham 1989]). Given that each response reflects complex attributes of behavior, physiology, and life history (op cit.), and because the response of related individuals at any one point in space and time is a product of their shared evolutionary history, when variation exists within the population in response to wetland drying, it raises the question of what factors maintain the variable responses.

Freshwater turtles are capable of terrestrial movement between wetlands (Gibbons et al. 1990, Graham et al. 1996), and by virtue of their low metabolic rates, ability to store water, and capacity for additional physiological adjustments to conserve energy and water, turtles are also well suited to remain dormant for extended periods (i.e., estivate) and await re-flooding (Kennett and Christian 1994, Peterson and Stone 2000, Ligon and Peterson 2002). Differences in propensity to reside or move to other wetlands have been reported among species of freshwater turtles at a common locality (Gibbons et al. 1983, Christiansen and Bickham 1989) and even among populations of a single species (Ligon and Peterson 2002). Examples of variation among individuals within a single population of freshwater turtles are less common (but see Gibbons et al. 1990), and to our knowledge no studies have examined factors that explain the existence of variable strategies or tactics within a population in the context of wetland drying. Here, we examine intrapopulation variation in terrestrial residency and inter-wetland movements and associated fitness costs and benefits of each behavior in a carnivorous freshwater turtle, *Chelodina longicollis*. Because the typical *C. longicollis* at our study site maintains associations with several wetlands and terrestrial habitats during a single year (Roe and Georges 2007), we define a population as the individuals occupying a localized group of wetlands instead of each wetland as harboring a demographically distinct sub-population. Animals that demonstrate such vagility are perhaps best defined as comprising "patchy populations" (Harrison 1991), and such a classification has been recently adopted to describe the dynamic population structure of similarly mobile freshwater turtles (Joyal et al. 2001, Bowne et al. 2006). By examining variation within a population, we aim to identify factors shaping behavioral variation in freshwater reptiles while

limiting, as much as possible, potentially confounding phylogenetic differences among individuals.

METHODS

Study site

Turtles were studied from September 2004 to March 2006 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) and Roe and Georges (2007). The site is characterized by forested terrestrial habitats and a mosaic of freshwater wetlands including several permanent dune lakes and a number of temporary swamps of various hydroperiods (duration of surface water presence; Fig. 1). Wetlands were continuously monitored for surface water presence from September to March of each year, corresponding to the turtle's activity season (Kennett and Georges 1990). Hydroperiod scores were calculated for each wetland by dividing the number of days surface water was present by the number of days monitored. Wetlands that remained continually flooded (hydroperiod score of 1.0) were classified as permanent, while wetlands that were known to have dried were classified as temporary. Temporary wetlands with a hydroperiod score between 0.5 and 0.9 were classified as intermediate, while those with a hydroperiod of <0.5 were classified as ephemeral.

Turtle capture

Turtles were captured using baited crab traps or by hand from wetlands distributed across the site. At each capture, we measured straight-line carapace length (CL) and plastron length (PL) to the nearest 0.1 mm using vernier callipers, and the mass of each turtle to the nearest gram. Turtles with CL < 145 mm were classed as juveniles, and for those with CL > 145 mm, we determined sex by examining the plastron curvature (see Kennett and Georges 1990). Each turtle was marked with a unique code by notching the marginal scutes of the carapace before release.

Radiotelemetry

Sixty adult turtles (39 female, 21 male) were fitted with radio transmitters (Sirtrack, 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. In order to capture variation resulting from the heterogeneity of wetlands at the study site, we studied individuals originally captured in eight different wetlands from two general regions of the site using radiotelemetry (18 turtles from wetlands in the northwest [Ryan's Swamp, Lake McKenzie, Windermere, and Claypits area] and 42 from wetlands in the southeast [Blacks Waterhole and Steamers Waterholes area]; Fig. 1). All wetlands were within an area enclosed by a circle with a 2.6 km radius, a distance that *C. longicollis* is capable of traversing between wetlands

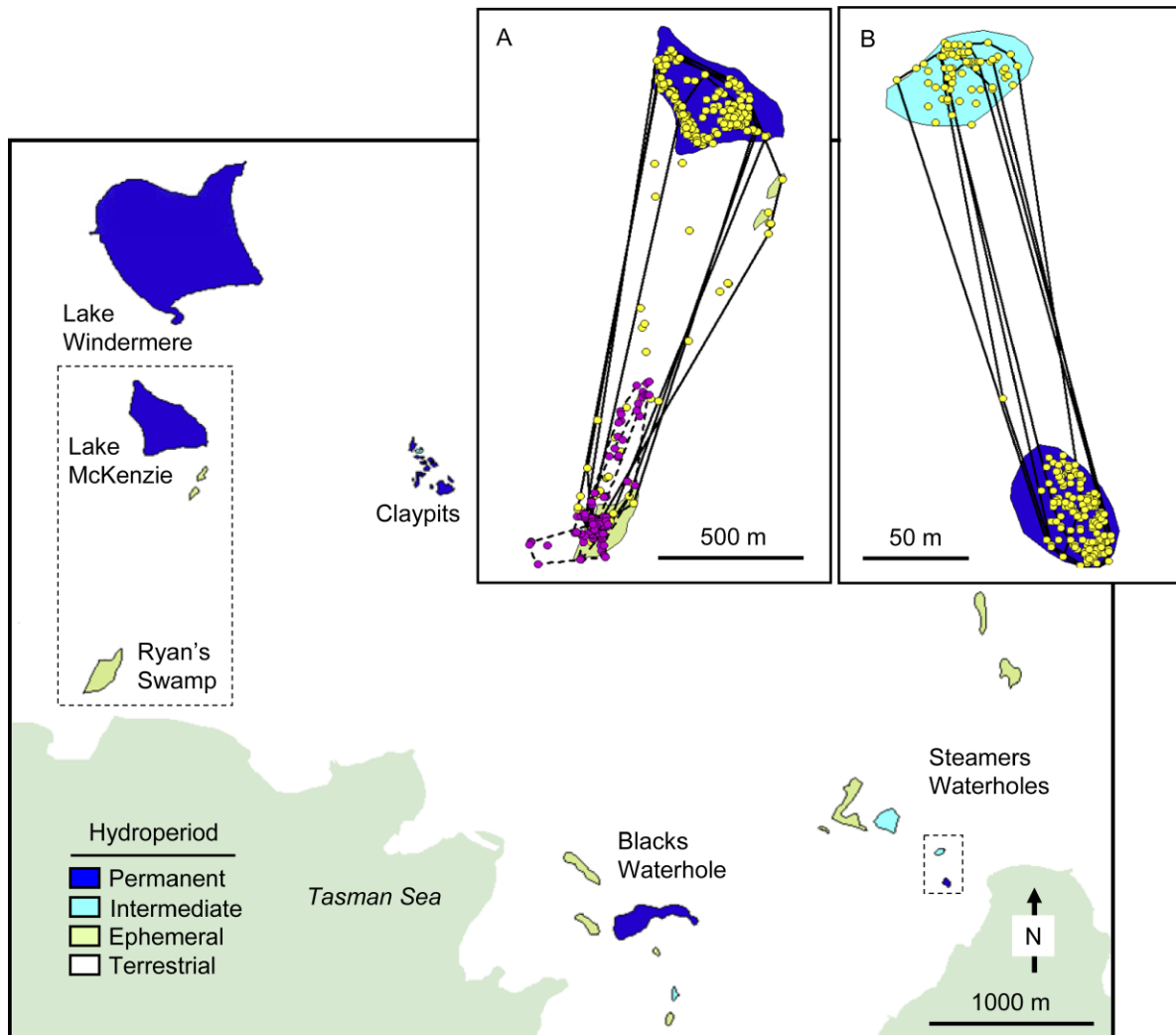


FIG. 1. Map of wetlands in Booderee National Park, southeastern Australia, showing hydroperiod. The insets show radio locations and minimum convex polygons for individual turtles (*Chelodina longicollis*) that moved to a permanent lake (yellow circles and solid lines) or resided terrestrially near the temporary wetland (magenta circles and dashed lines) in two subregions of the study: (A) Lake McKenzie and Ryan's Swamp, and (B) Steammers Waterholes. Detailed locations and movements could not be shown for all 60 turtles without obscuring the map. Note the difference in scale between insets and between insets and the larger map.

(Kennett and Georges 1990; J. H. Roe, *unpublished data*). Initial carapace length and mass of males ranged from 162.9 to 193.5 mm and 410 to 653 g, while females ranged from 171.0 to 218.9 mm and 510 to 1004 g. Transmitters ranged from 2.5% to 6.1% of the turtle's body mass.

Turtles were located 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 (GPS III Plus, Garmin, Olathe, Kansas, USA) or from distance and bearing measurements to known locations. Coordinate positions determined by GPS units had an error of 1–7 m. Location coordinates were then plotted on habitat

maps using ArcView GIS 3.1 (Environmental Systems Research Institute 1992). We classified each location as being in either a terrestrial habitat or wetland, and calculated two measures of terrestrial behavior for each individual: (1) proportion of locations in terrestrial habitats and (2) terrestrial duration (the number of consecutive days spent in terrestrial habitats without returning to water). We also calculated two scores for each turtle to reflect (1) mean hydroperiod score of all wetlands used by the turtle throughout the radio-tracking period and (2) straight-line distance to the nearest permanent wetland from the most distant temporary wetland used by the turtle. Distances between the closest edges of wetlands were estimated using the Nearest Features extension for Arc View GIS.

Growth and body condition

We conducted a capture–mark–recapture study using the capture techniques described previously. We assessed growth patterns and changes in body condition of recaptured individuals. In this study, we only report on growth and body condition of recaptured turtles from two permanent lakes (Lakes McKenzie and Windermere) and one temporary swamp (Ryan's Swamp) in order to facilitate comparisons with Kennett and Georges (1990). Growth was measured as the change in CL between captures, and growth rates were calculated by dividing change in shell length by the fraction of the approximately six-month growing season (15 September–15 March) elapsed between initial and final captures. We only included individuals in the analyses if the period between captures spanned at least one-half of a growing season, and only if both captures were in the same wetland. Individuals were assumed to have grown appreciably only if the growth increment exceeded the accuracy of measurements (± 0.5 mm); where the growth increment was < 0.5 mm, individuals were considered not to have grown appreciably and were omitted from analyses of growth rate. The proportion of individuals that grew appreciably was also determined for each wetland. All calculations and analyses of growth were done in accordance with that of Kennett and Georges (1990) to enable direct comparisons between studies.

Data analysis

Statistical analyses were performed with SAS Version 8.2 (SAS Institute 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. Statistical significance was accepted at the $\alpha \leq 0.05$ level except when stated otherwise.

To investigate factors influencing variation in terrestrial behavior among individuals, we used linear and quadratic multiple regression analyses. As previous investigations detected no differences between sexes in terrestrial habitat use or movement (Roe and Georges 2007), males and females were included together in our analyses. Additionally, individuals in both the northwest and southeast regions of the site were grouped together in analyses even though turtles do not regularly move between these regions, though movements among wetlands within both regions are frequent (Roe and Georges 2007). Due to the proximity of these regions to one another and the similarity in movement and habitat use behaviors of turtles in these regions, the regions were grouped to increase sample size and power of our analyses. We assessed how four independent variables influenced each of four dependent variables reflecting terrestrial habitat use. The independent variables were: (1) maximum distance between temporary and permanent wetlands, (2) mean hydroperiod score, (3) turtle size (PL), and (4) condition index (mass adjusted for PL,

calculated as g/mm^b , where b is the scaling exponent from a regression of \log_{10} body mass [in grams] on \log_{10} PL [in millimeters]) (see Peterson and Stone 2000). The dependent variables were (1) percentage of terrestrial locations, (2) maximum terrestrial duration, (3) variation in percentage of terrestrial locations, and (4) variation in maximum terrestrial duration. The Dunn-Sidak method was applied to this family of multiple regressions to constrain the experiment-wide Type I error to 0.05 (Quinn and Keough 2002). The α level for statistical significance for each test was $\alpha \leq 0.013$. The percentage of terrestrial locations was arcsine square-root transformed, and we added a value of 1 to terrestrial duration before \log_{10} -transformation to accommodate zero values. Variation in terrestrial habitat use was assessed by grouping individuals into 100-m distance and 0.1-hydroperiod score classes and calculating the standard deviation for each variable within each class. Variation was only assessed for classes with at least two individuals. Each dependent variable was examined against all independent variables together in separate analyses. Because we detected variance inequalities for the relationship between proportion of terrestrial locations and distance to permanent wetlands (see *Results*), we used a weighted regression with distance^{-1.2} as the weighted variable. For multiple regression, we dropped terms with $P > 0.10$, then used multiple or simple regression models to reassess relationships between the dependent and the remaining independent variables at the $\alpha \leq 0.013$ level. We compared survival of radio-tracked turtles that migrated to or remained in permanent wetlands following wetland drying to those that remained at temporary wetlands with Fisher's exact tests.

Growth and body condition of adults and juveniles were examined in three wetlands (Lakes McKenzie, Windermere, and Ryan's Swamp). The proportion of individuals (juveniles and adults separate) showing appreciable growth was compared between wetlands with a series of Fisher's exact tests, and growth rates were compared between wetlands using ANCOVA, with wetland as the independent variable, \log_{10} carapace growth rate as the dependent variable, and initial CL the covariate. To examine changes in body condition for all turtles (juveniles and adults combined), we examined the relationship between mass (dependent variable) and PL (covariate) between initial and final captures of individuals using repeated-measures ANCOVAs with compound symmetry covariance structure (PROC MIXED Model, SAS, version 8.2, SAS Institute 1999). This analysis assumes an animal in good condition would have a greater mass than an animal of the same PL in poor condition.

RESULTS

Terrestrial behavior and survival

Terrestrial behavior was highly variable among individuals (Figs. 1 and 2), with percentage of terrestrial

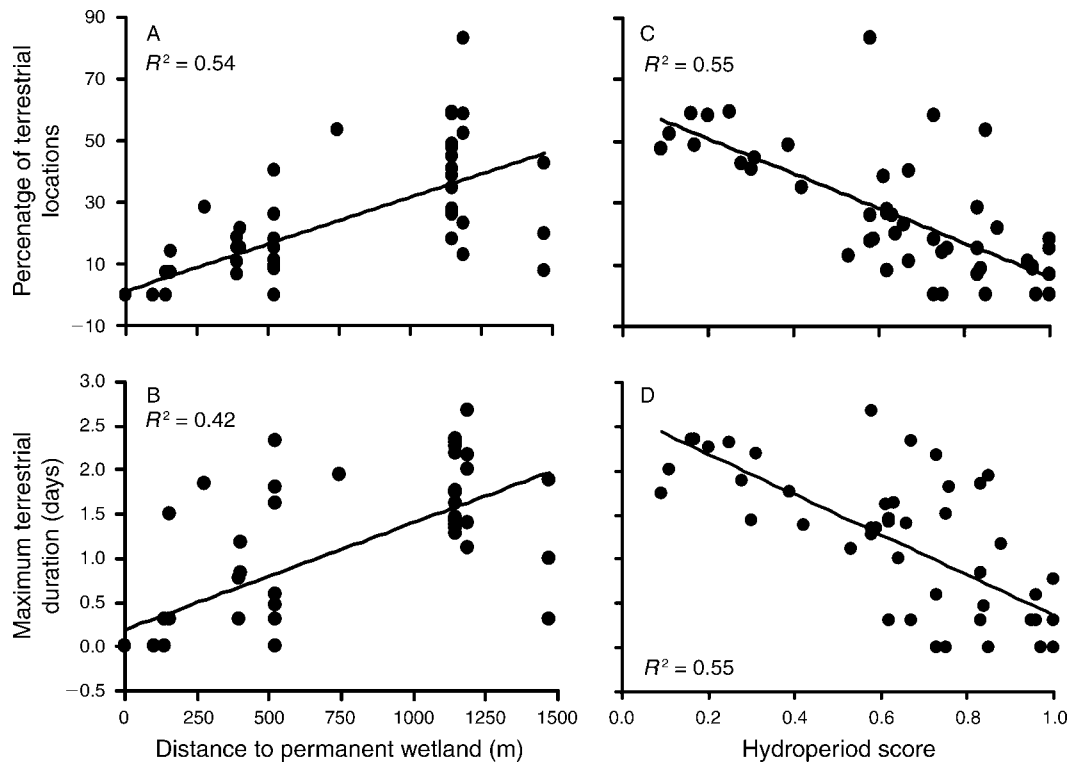


Fig. 2. Relationships between terrestrial behavior of *Chelodina longicollis* and (A, B) distance from temporary wetlands to the nearest permanent wetland, and (C, D) wetland hydroperiod. Percentage of terrestrial locations was arcsine square-root transformed, and we added a value of 1.0 to terrestrial duration before \log_{10} -transformation prior to analyses. Hydroperiod score is the proportion of time that surface water was present in the wetland, with a score of 1 reflecting wetlands that remained continually flooded, and a score of 0 reflecting wetlands that never flooded.

locations ranging from 0 to 99%, and maximum terrestrial duration ranging from 0 to 480 days. Because hydroperiod score and distance from temporary to the nearest permanent wetland were significantly correlated ($r^2 = 0.59$, $F_{1,52} = 72.61$, $P < 0.001$), we ran two separate regression analyses to avoid complications of collinearity of independent variables, in addition to stepwise regression with both variables included in the model. This collinearity is likely an artifact of the spatial arrangements of wetlands within the watersheds at our site; the more permanent wetlands tended to be lower in the catchments and thus functioned as collector pools, while those higher in the catchments (i.e., farther from the permanent collector pools) drained and dried more quickly.

The percentage of terrestrial locations increased linearly with increasing distance between temporary and permanent wetlands ($r^2 = 0.54$, $F_{1,52} = 57.63$, $P < 0.001$; Fig. 2) and was due to both an increase in terrestrial duration ($r^2 = 0.42$, $F_{1,52} = 37.18$, $P < 0.001$; Fig. 2), and an increase in the percentage of turtles residing at temporary wetlands ($r^2 = 0.74$, $F_{1,6} = 14.32$, $P = 0.013$). At the two extremes, 100% of turtles using temporary and permanent wetlands separated by <100 m moved to permanent wetlands, but at a distance of 1400–1500 m, 67% of turtles resided in or near the

temporary wetland following wetland drying. Percentages of terrestrial locations and terrestrial duration also increased linearly with decreasing hydroperiod ($r^2 > 0.55$; $F_{1,52} > 62.64$, $P < 0.001$; Fig. 2). Both distance and hydroperiod ($P < 0.006$) were significant predictors of the percentage of terrestrial locations in a stepwise regression, but hydroperiod ($P < 0.001$) and not distance ($P = 0.185$) was significant for terrestrial duration. Neither turtle size nor body condition was a significant predictor of terrestriality in any model ($P > 0.067$).

The analysis of variation in terrestrial habitat use (measured as the standard deviation [SD] within each class) included 51 individuals representing seven distance classes spanning the entire range of distances between permanent and temporary wetlands (0–100 m to 1400–1500 m), and 51 individuals representing eight hydroperiod classes spanning nearly the full range of wetland hydroperiod scores (0.1–0.2 to 0.9–1.0). Variation in the proportion of terrestrial locations increased linearly with increasing distance between temporary and permanent wetlands ($r^2 = 0.90$, $F_{1,6} > 47.22$, $P = 0.001$; Fig. 3), but no relationship was found between variance in terrestrial duration and distance between wetlands ($P = 0.095$). Hydroperiod score was not a significant

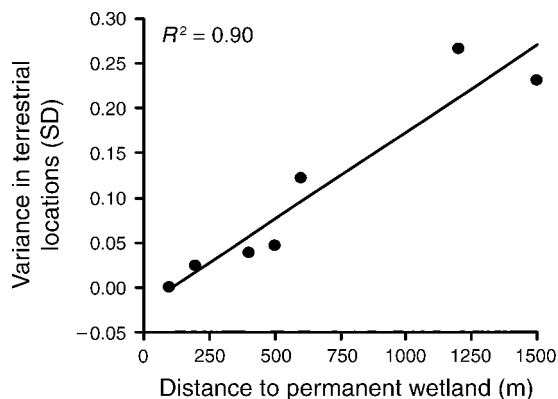


FIG. 3. Relationship between variance in *Chelodina longicollis* terrestrial behavior and distance from temporary to permanent wetlands. Variance is measured as the standard deviation (SD) of the proportion of terrestrial locations for each distance class.

predictor of variance in either aspect of terrestrial behavior examined ($P > 0.385$).

Survival of radio-tracked turtles that moved to or remained within permanent wetlands (82%) was higher than those that remained at temporary wetlands (55%) following wetland drying ($P = 0.038$). Of the 10 individuals (7 female, 3 male; 162.9–215.5 mm CL) that died while residing at temporary wetlands, one was preyed upon by an eagle (*Aquila audax* or *Haliaeetus leucogaster*), one was hit by a vehicle along a service track, while the other eight eventually failed to bury in the substrate and were visibly emaciated prior to death. These observations suggest death from starvation and/or dehydration, but blood properties and body composition were not monitored and thus cause of death could not be confirmed (Peterson and Stone 2000). Of the seven individuals (4 female, 3 male; 168.0–206.0 mm CL) that died while moving back to or remaining within permanent wetlands, three were preyed upon by eagles and the cause of death was undetermined for the other four. No sex or body size differences were detected among those that died in residency at temporary wetlands ($P > 0.296$) nor for those that moved to or remained within permanent wetlands ($P > 0.511$).

Growth and body condition

Two-hundred seventy turtles (217 adults, 53 juveniles) from the Lake McKenzie, Windermere, and Ryan's

Swamp complex were recaptured in their wetland of original capture. The percentage of juveniles and adults showing appreciable growth did not differ among wetlands ($P > 0.103$; Table 1). Average adult growth rates did not differ among wetlands (Table 1), but after correcting for body size, the ANCOVA detected an interaction between CL and wetland for adult growth rate (CL, $F_{1,53} = 0.02$, $P = 0.891$; wetland, $F_{2,53} = 6.12$, $P = 0.004$; CL \times wetland, $F_{2,53} = 5.98$, $P = 0.005$). Growth rates of Lake Windermere adult turtles decreased with increasing body size ($n = 24$, $R^2 = 0.50$) and increased with increasing body size in Ryan's Swamp ($n = 3$, $R^2 = 0.97$), but rates did not differ significantly among body sizes in Lake McKenzie ($n = 32$, $R^2 = 0.08$). The relationship between juvenile growth rate and size also varied between wetlands (CL, $F_{1,20} = 0.23$, $P = 0.635$; wetland, $F_{1,20} = 5.48$, $P = 0.030$; CL \times wetland, $F_{1,20} = 5.69$, $P = 0.027$). Juvenile growth rate decreased with increasing size in Lake McKenzie ($n = 16$, 96.4–143.0 mm CL; $R^2 = 0.46$), but did not vary with size in Lake Windermere ($n = 8$, 129.6–144.7 mm CL; $R^2 = 0.35$), most likely an artifact of the relatively narrow size range. Because no juveniles in Ryan's Swamp grew appreciably, this wetland was excluded from this analysis. Although only four juveniles were recaptured in Ryan's Swamp, these individuals represented a wide size range (89.6–144.9 mm CL), which should have allowed for detection of any growing individuals had growth occurred.

Changes in body condition differed among wetlands. Turtles in Lake McKenzie increased body condition by 1.1% regardless of size ($\log_{10}PL$, $F_{1,150} = 5305.26$, $P < 0.001$; condition, $F_{1,150} = 6.37$, $P = 0.013$), whereas turtles in Ryan's Swamp decreased body condition by 7.7% regardless of size ($\log_{10}PL$, $F_{1,20} = 3367.50$, $P < 0.001$; condition, $F_{1,20} = 22.25$, $P < 0.001$). In Lake Windermere, there was an interaction between body size and body condition change, but body condition change ranged between -2.0% and $+0.8\%$ ($\log_{10}PL$, $F_{1,94} = 3322.72$, $P < 0.001$; condition, $F_{1,94} = 6.10$, $P = 0.015$; $\log_{10}PL \times$ condition, $F_{1,94} = 5.84$, $P = 0.018$).

DISCUSSION

The *C. longicollis* population exhibited a high degree of variation in terrestriality, reflecting alternate strategies or tactics of individuals in response to wetland drying. Some turtles immediately move to permanent wetlands while others reside terrestrially near temporary

TABLE 1. Growth of adult (A) and juvenile (J) turtles (*Chelodina longicollis*) from two permanent lakes and a temporary swamp in Booderee National Park, southeastern Australia.

Wetland	Recaptures (<i>n</i>)		Percentage growing		Carapace growth rate (mm/yr)†	
	A	J	A	J	A	J
Lake McKenzie	119	34	29.4	47.1	1.04 \pm 0.13 [0.11–3.21]	1.47 \pm 0.37 [0.53–5.27]
Lake Windermere	80	15	28.8	53.3	1.09 \pm 0.17 [0.25–3.38]	1.34 \pm 0.31 [0.66–3.25]
Ryan's swamp	18	4	16.7	0.0	0.89 \pm 0.05 [0.81–0.98]	0.00 [0.00–0.00]

† Because growth rates were size dependent in some cases, we present both mean \pm SE and range.

wetlands for various lengths of time. Both wetland hydroperiod and proximity to other more permanent bodies of water accounted for some of the behavioral variation, but variance still existed among individuals occupying the same wetlands. That such variation in response to wetland drying exists among individuals in the same population (i.e., using the same set of wetlands) suggests individuals may differentially weigh the benefits of one strategy or tactic against the costs of the other, and raises the question as to what ultimately maintains this behavioral variation.

Both movements to other wetlands and residency within or near dry wetlands to await more favorable conditions have potential costs and benefits. Costs of residing within the dry wetland or in nearby terrestrial habitats include depletion of energy and water stores (Ligon and Peterson 2002) or death from exposure to extreme conditions should the wetland remain dry for long periods (Christiansen and Bickham 1989, Bodie and Semlitsch 2000). However, if the wetland soon re-floods, individuals in close proximity would maximize foraging opportunities by being first to take advantage of the bloom of aquatic productivity typical of recently flooded wetlands (Brinson et al. 1981), even for short duration flooding events, without incurring the high costs of terrestrial movement. Costs of movement to other wetlands include increased mortality risk from predators (Spencer and Thompson 2005) and roads (Aresco 2005), energy expenditure (Stockard and Gatten 1983), time, and the potential cost of lost foraging opportunities if the wetlands they evacuated soon re-flood. However, should temporary wetlands remain dry, movement to the low productivity permanent lakes (Georges et al. 1986, Kennett and Georges 1990) would allow for at least some continued foraging elsewhere and avoidance of the costs of remaining at temporary wetlands. It becomes apparent that the relative costs and benefits of residing or moving to other wetlands would be contingent upon whether temporary wetlands quickly re-flood or remain dry for extended periods.

In our study, terrestrial estivation (defined here as terrestrial inactivity during dry periods, Gregory 1982) was a facultative behavior dependent in part on both local (wetland hydroperiod) and landscape (distance between wetlands) factors, but not attributes of the turtles themselves such as size, sex, or the body condition index. The negative relationship between terrestrial habitat use and wetland hydroperiod is likely a result of individuals maximizing resource acquisition in wetlands for as long as flooded conditions permit, as most freshwater turtles, including *C. longicollis*, rarely if ever feed on land (J. H. Roe, unpublished data). That more individuals declined to move to permanent wetlands by remaining terrestrial for longer times when temporary and permanent wetlands were farther apart is perhaps reflective of the perceived high costs and risks of long distance overland movement. When only short distances must be traveled, the costs of round-trip

migration between temporary and permanent wetlands would be low relative to the potentially high costs of residing at dry wetlands (e.g., depletion of energy stores, death), but for turtles using more distant temporary wetlands (up to 1.5 km in this study), the high costs and risks of a round-trip journey (e.g., energy expenditure, predation) may be incentive to delay or forego a trek altogether and await the return of flooding. That the relationship between terrestriality and both local and landscape habitat variables have nonzero slopes suggests that terrestriality is in part a behaviorally plastic response (sensu Stearns 1989), and that competition for resources and the behavior of others (i.e., a frequency-dependent decision) was less of a factor in explaining the chosen strategy or tactic. If individuals were simply behaving based on the choices already made by others, we would expect to see a similar distribution of behaviors among individuals at temporary wetlands regardless of wetland isolation or hydroperiod, which was not the case. We also found little evidence for synchrony of movements from drying wetlands among individuals at a particular wetland, beyond that which can be attributed to rainfall (J. H. Roe, unpublished data). This observation suggests individuals are not directly following one another in their behavioral decisions.

Even though some *C. longicollis* survived extended terrestrial estivation (up to 480 consecutive days) while awaiting re-flooding, a large proportion (45%; irrespective of adult size or sex) died, compared to lower mortality rates (18%) of those that moved to permanent wetlands. In light of these extreme consequences, the existence of any behavioral variation in response to wetland drying is at first puzzling. To provide additional insight on potential causes of this variation, we examined historical patterns of a critical environmental factor. Annual rainfall has fluctuated widely and unpredictably, with years of high rainfall as much as 4.3-fold above years of low rainfall at our site (Fig. 4). Although we do not know the complete history of flooding and drying patterns of temporary wetlands at our site, the limited data we have come from observations at Ryan's Swamp from 1983 to 1987 (a relatively wet period; 1288 mm/yr), and again from 2004 to 2006 (a relatively dry period; 886 mm/yr; Fig. 5). During the wet period, the swamp fluctuated between depths of 0.8–1.5 m but was never observed to completely dry, and during the dry period it was dry for 82% of the active seasons (September–March), with a maximum hydroperiod of only 30 days and depth of 0.22 m. The observations during these two periods, together with evidence from other studies demonstrating a strong correlation between annual precipitation and wetland hydroperiod (Bauder 2005) suggest that temporary wetlands at our site have historically flooded and dried in a pattern reflective of the unpredictable precipitation. We then asked the question of whether this environmental variability also translates into variation in the

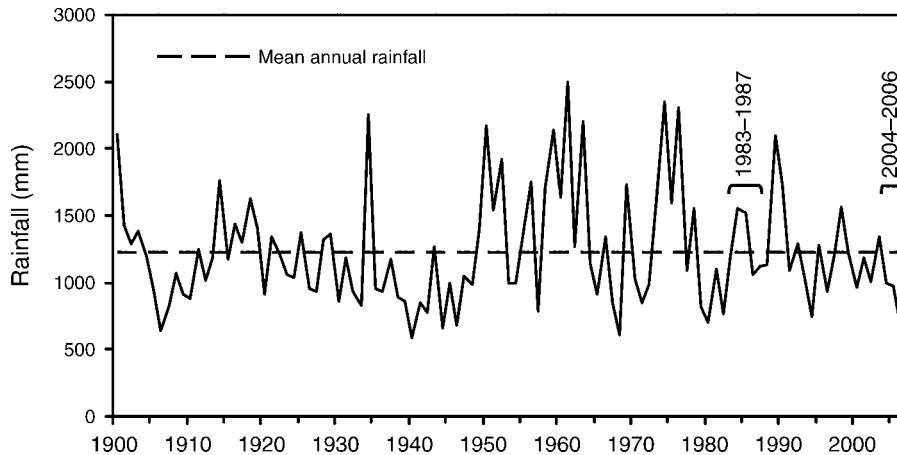


FIG. 4. Historical annual rainfall variation from 1900 to 2006, at the Point Perpendicular weather station (Australian Bureau of Meteorology) located ~13 km north of our study site. As our study encompassed only three months of 2006 (January–March), we projected annual rainfall for this year by multiplying total rainfall during this period by 4. Brackets indicate the period of our study (2004–2006) and that of Kennett and Georges (1990), 1983–1987.

costs and benefits to turtles moving to permanent wetlands or residing at temporary wetlands once wetlands dry.

Indeed, several life history traits and condition indices with fitness consequences differed markedly between turtles in temporary and permanent wetlands, but the higher quality habitat shifted between wet and dry periods. During the wet period, body condition, juvenile and adult growth, as well as reproductive output were considerably higher in the temporary wetland than in the nearby permanent lakes, reflecting the higher productivity of temporary wetlands at this time (Kennett and Georges 1990). In contrast, during the dry period, turtle body condition declined by nearly 8%

between recaptures in the temporary wetland compared to relatively little change (–2% to +1%) in the permanent lakes, and adult and juvenile growth rates were similarly low in both permanent and temporary wetlands (Table 1). We hypothesize that the large production benefits offered in temporary wetlands over permanent lakes during wet periods (Kennett and Georges 1990) weighed against the potential costs of long-distance overland movement would select for maximization of time in or near these distant temporary wetlands (residency) even throughout short duration or near-drying events. During dry periods, when temporary wetlands no longer offer production benefits, the survival and body condition payoffs in permanent lakes would select for

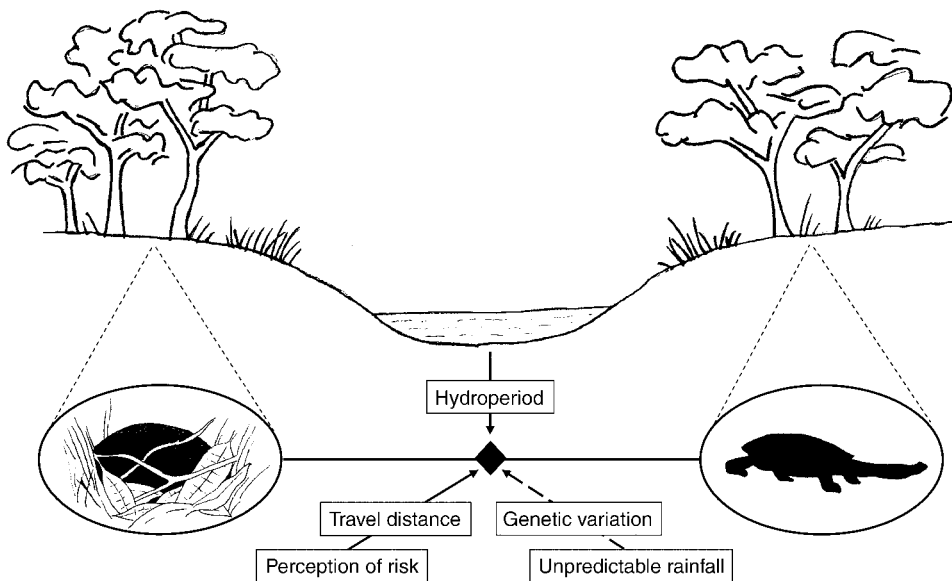


FIG. 5. Factors influencing the decision to estivate, how long to estivate, or whether to move to permanent wetlands for the freshwater turtle *Chelodina longicollis*. The dashed arrow represents an hypothesized link, but other factors may also contribute.

movements to the lakes at this time. During extended periods of extremes such as multiyear droughts or continuous wet (1979–1982 or 1958–1964, respectively; Fig. 4), persistent fitness payoffs of one response over another would likely lead toward fixation of a behavior, but due to the historical unpredictability of rainfall, individuals would not have reliable information on which to anticipate the best response for the immediate future. Under this scenario both behaviors could coexist as is predicted by Giesel (1976), as a propensity to escape wetland drying in space (move to other wetlands) or in time (estivate) becomes a bet-hedging strategy maintained by in part genetic variation. Underlying genetic variability could theoretically reflect a dichotomous polymorphism or a continuum of heritable environmental switch points or thresholds that differ among individuals (Lack 1968, Lundberg 1987). Although the different responses have clear fitness consequences, before giving weight to the role of genetics in explaining the ultimate maintenance of variable responses observed here, we would need to demonstrate that the turtles' responses are also in part genetically determined (i.e., heritable). It is plausible that behavioral decisions are influenced by other factors that we could not examine such as age, experience, hatching site, or more robust measures of body condition that measure lipid stores.

CONCLUSIONS

We provide an example of intrapopulation diversity on a small spatial scale in the behavioral response to wetland drying for a freshwater reptile, and are the first to examine factors contributing to such variability in the field. These findings, together with recent laboratory studies (Peterson and Stone 2000, Ligon and Peterson 2002), demonstrate substantial behavioral and physiological variation in response to simulated and real drying conditions among individuals within a population of freshwater turtles. Moreover, both our field study and other laboratory studies (op cit.) link substantial fitness consequences with terrestrial estivation and movement to other wetlands in turtles, indicating that aspects of behavior in oscillating environments, such as habitat choice, are subject to natural selection.

We identify three factors likely to be instrumental in shaping the behavioral response of freshwater reptiles inhabiting wetlands that periodically dry: (1) wetland hydroperiod, (2) the perceived cost of travel, and (3) predictability of environmental variation (Fig. 5). Where temporary wetlands are isolated from other bodies of water by long distances or other barriers that may increase risk, and where flooding duration is short, we expect the proportion of residential individuals in a population to increase relative to regions where wetlands are more spatially clustered and permanently flooded. We hypothesize that in areas characterized by stochastic environmental variation (e.g., precipitation) where wetlands flood and dry erratically, behavioral variation

in response to wetland drying may be maintained, though the ratio of individuals exhibiting a particular strategy or tactic will vary to reflect the relative success of that strategy or tactic over others during recent environmental conditions. We demonstrate that a holistic understanding of behavioral variation must consider several factors simultaneously, and that long-term or repeat studies of a single population may be necessary to capture the wide variability of environmental conditions that have shaped a population's behavior over time.

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