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Covariates streamline age-specific early life survival estimates of two chelonian species

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Abstract

Delayed maturity and high survival rates of immatures and adults characterize long-lived species' life histories. Understanding how these traits interact in stochastic environments is essential to understand early life in long-lived species and to assist conservation planning. Unfortunately, available information of demographic traits in immatures are often fragmentary and the logistical difficulties of capturing and recapturing this cohort leave little room for improvement. Published immature chelonian survival estimates vary broadly, are often not age-specific, and lack precision. In an attempt to overcome this issue, we developed a novel modelling approach based on Capture-Recapture data to obtain robust age-specific survival probabilities in two chelonian species (the freshwater European pond turtle, *Emys orbicularis*, and the terrestrial Hermann's tortoise, *Testudo hermanni*). More specifically, we show that implementing a linear relationship between survival probabilities and age does not distort survival estimates and improves precision. Both species display a progressive increase in survival with age, reaching a plateau at the ages of four to five. As maturity occurs later in both species (8–12 years-old), the survival plateau might be governed by the final hardening of the carapace, which brings obvious survival benefits. Taking advantage of the flexibility of multievent models we encourage a systematic field approach even when very large samples from immatures cannot be amassed. Only so can demographic traits in chelonians, and more generally in long-lived species, be properly explored.

Introduction

Delayed sexual maturity, high immature and adult survival, and variation in the correlative nature of these traits define the life histories of long-lived animals (Dunham, Miles & Reznick, 1988; Charnov, 1990; Congdon, Dunham & van Loben, 1993; Congdon, Dunham & van Loben Sels, 1994). Understanding their ecology, evolution and finally conservation biology requires robust demographic analyses based on thorough insight on these traits (Heppel, 1998; Enneson & Litzgus, 2008). Nevertheless, developmental changes throughout a prolonged immature phase can induce huge variation in trait values; e.g. before (delayed) maturity mean annual survival increases linearly with age (see for instance Congdon et al., 1994; Jorgenson et al., 1997; Fernández-Chacón et al., 2011; Hastings et al., 2011; DeLong et al., 2017). This complicates the understanding of trait covariation and mandates age-, or at least stage-specific estimates.

Longevity and delayed maturity are often expressed to the extreme in chelonians (Wilbur & Morin, 1988). At present day, an ever-increasing set of threats (Klemens, 2000) have made that combination of life-history traits a chelonian Achilles' heel, with almost 70% of all 335 species threatened or recently extinct (almost 46% of which endangered or critically endangered); for many, conservation status has not been assessed (van Dijk et al., 2014). In order to counter this trend robust age-specific survival estimates are necessary to provide age-specific survival elasticities. Indeed, developing reliable projections of population growth using matrix models (Caswell, 2001), evaluating conservation priorities (Congdon et al., 1993; Heppel, 1998; Enneson & Litzgus, 2008) and estimating conservation efficiency (e.g. after reintroduction and/or headstarting in Heppel, Crowder & Crouse, 1996a; Mitrus, 2005; Canessa et al., 2016) rely on such endeavours in long-lived animals.

Alas, the elusive nature of chelonian early life precludes the amassing of large and dense CR (Capture-Recapture) datasets of aged immature turtles, actively hindering this goal. Although chelonian adult survival is relatively well-studied (Congdon et al., 1994; Henry et al., 1999; Chaloupka & Limpus, 2005; Olivier et al., 2010; Bertolero et al., 2011; Bertolero, Pretus & Oro, 2018), sporadic insight on early survival fails to paint a clear picture. Indeed, a rapid review of the sparse literature on age-specific early life chelonian survival revealed a wide spectrum of estimates ranging from 11% in neonate European pond turtles (*Emys orbicularis*) to 92% in juvenile Loggerhead turtles (Table 1). Much is likely a Alas, the elusive nature of chelonian early life precludes the amassing of large and dense CR (Capture-Recapture) datasets of aged immature turtles, actively hindering this goal. Although chelonian adult survival is relatively well-studied consequence of inherent interspecific differences; in juvenile tortoises survival estimates range from eight to 90%, whereas in juvenile sea turtles they almost always exceed 70% (Table 1). Perhaps even more importantly, the plethora of methodological approaches (last column, Table 1) likely contributes largely to this variation (see also Pfaller et al., 2018).

Tableau 1 Review of published chelonian age- or stage-specific survival estimates prior to maturity. Some studies reported ambiguous age categories here presented as immature. When explicitly reported, materials and methods are also provided

Species	Immature (age-specific) survival	Materials & methods	Reference
Land tortoises			
T. h. hermanni	Neonate: 0.39 \pm 0.10 1-year-old: 0.45 \pm 0.08 2-year-old: 0.77 \pm 0.08 3-year-old: 0.68 \pm 0.07 4-year-old: 0.86 \pm 0.06 5-year-old: 0.88 \pm 0.05	19 years of CR, Cormack-Jolly-Seber (CJS) model	Fernandez-Chacbn et al. (2011)
T. h. hermanni	Neonate: 0.54 1–2 years-old: 0.64 3–9 years-old: 0.91	14 years of CR, CJS model	Bertolero (2002)
T. h. hermanni	0–2 years-old: 0.52 3–9 years-old: 0.88	7 years of CR	Henry et
Testudo graeca	Neonate: 0.39	Thread trailing	Keller, Diaz-Paniagua & Andreu (1998)
Gopherus polyphemus	1–4 years-old: 0.45	/	Wilson (1991)
Gopherus polyphemus	Immature: 0.84 Fernandez-Chacon	12 years of CR, CJS open population model	Tuberville et al. (2008)
Freshwater turtles			
Emys orbicularis	Neonate: 0.02–0.08 1 year-old: 0.53 2 years-old: 0.80 3–6 years-old: 0.45–0.99 7–11 years-old: 0.55–1.15 12+ years old: 0.68–1.69	7 years of CR, CJS model	Canessa et al. (2016)
Emys orbicularis	Neonate: 0.11 1-year-old: 0.64	3 years of CR	Mitrus (2005)
Emys orbicularis	1-year-old: 0.53	/	Mitrus (2002)
Emys orbicularis	3–9 years-old: 0.80	/	Mitrus & Zemanek (2004)
Trachemys scripta	Immature: 0.83	/	Frazer, Gibbons & Greene (1990)
Myuchelys georgesi	Immature: 0.58	/	Blamires et al. (2005)
Chelydra serpentina	Immature: 0.75	/	Cunnington & Brooks (1996)
Chelydra serpentina	Immature: 0.65–0.82	/	Congdon et al. (1994)
Chrysemys picta	Immature: 0.81	/	Wilbur (1975)
Chrysemys picta	Immature: 0.83	/	Mitchell (1988)
Emydoidea blandingii	Immature: 0.78	/	Congdon et al. (1993)
Kinosternon flavescens	Immature: 0.64	/	Iverson (1991)
Kinosternon subrubrum	Immature: 0.72	/	Frazer, Gibbons & Greene (1991)
Clemmys guttata	Neonate: 0.81	30 years of CR, CJS model	Enneson & Litzgus, 2008;
Marine turtles			
Caretta caretta	Immature: 0.72	Catch-curve analysis	Bjorndal, Bolten & Martins (2003b)
Caretta caretta	Immature: 0.70	Catch-curve analysis	Frazer (1987)
Caretta caretta	Immature: 0.89	Catch-curve analysis	Epperly et al. (2001)
Caretta caretta	Immature: 0.83	CJS model	Heppell et al. (1996b)
Caretta caretta	Immature: 0.86/0.92	CJS model	Chaloupka & Limpus (2002)
Chelonia mydas	1-year-old: 0.91 \pm 0.03 2-year-old: 0.85 \pm 0.05 3-year-old: 0.91 \pm 0.04 4-year-old: 0.76 \pm 0.03	23 years of CR, Burnham model	Bjorndal, Bolten & Chaloupka (2003a)
Chelonia mydas	Immature: 0.88/0.85	CJS model	Chaloupka & Limpus (2005)
Chelonia mydas	Immature: 0.83	13 years of CR, CJS model	Patricio et al. (2011)
Chelonia mydas	Immature: 0.88 \pm 0.02	9 years of CR, CJS model	Chaloupka & Limpus (2005)

Here, we present a general analytical framework that allows for age-specific survival estimates to be obtained from sparse CR data (i.e. small and varying numbers of individuals per age class). We applied this approach on two distantly related (within Testudinoidea in Crawford et al., 2014), Near Threatened (IUCN 2017) chelonians: the European pond turtle and the Hermann's tortoise (*Testudo hermanni*). In *T. h. hermanni* (the western subspecies) age-specific survival progressively increases with age from 39% in neonates to 97% in 6-year olds and older (Fernandez-Chacon et al., 2011); juvenile survival estimates of its eastern counterpart (*T. h. boettgeri*) are lacking. Immature European pond turtle survival exhibits a very wide range (11% to 90% in Table 1), and robust age-specific analyses are lacking.

M1	Males from Esquineau/the Plateau with high recapture probability
m1	Males from Esquineau/the Plateau with low recapture probability
F1	Females from Esquineau/the Plateau with high recapture probability
f1	Females from Esquineau/the Plateau with low recapture probability
M2	Males from Faïsses/the Beach with high recapture probability
m2	Males from Faïsses/the Beach with low recapture probability
F2	Females from Faïsses/the Beach with high recapture probability
f2	Females from Faïsses/the Beach with low recapture probability
†	Dead

Tableau 2 Abbreviations (left column) and descriptions (right column) of states that European pond turtles from Camargue (Esquineau and Faïsses), France and Hermann's tortoises from Golem Grad (the Plateau and the Beach), Macedonia can assume and transit among

Materials and methods

Studied species and sites European pond turtle

The European pond turtle inhabits a broad range of habitats across Europe, northern Africa and westerns Asia. Nevertheless, it is often locally endangered and even extinct (Fritz & Chiari, 2013). The European pond turtle is largely impacted by diverse anthropogenic factors such as habitat loss, regulation of rivers and shoreline development that homogenize habitats and fragment populations (Rogner, 2009).

During 16 years (1997–2012), a total sampling hand-capture effort of 598 h and 6158 trap-days in the Natural Reserve of Tour du Valat (Camargue, France, 250 ha 43°30'N, 4°40'E) resulted in 749 captured European pond turtles (for details on field methodology see Olivier et al., 2010 and Fichoux et al., 2014). Among these, 298 could be aged using growth-rings (Castanet, 1988; Olivier, 2002) for a total of 809 captures. Sex was assigned for sexually dimorphic individuals followed by permanent notch marking on the carapace (Cagle, 1939).

Hermann's tortoise

Hermann's tortoises are widespread across the European Mediterranean region. Nevertheless, the westerns subspecies has suffered major losses in habitat and therefore distribution range (Stubbs, 1995; Bertolero et al., 2011). With rapid uncontrolled urbanization in the Balkans, its eastern counterpart might be heading for a similar fate. Local illegal and legal tortoise harvest of huge proportions in the past decades (Cites trade report on *Testudo hermanni*, 2017) have massively contributed to this trend.

During 9 years (2008–2016), we studied a very dense (~60 adults per hectare, Bonnet et al., 2016) population on Golem Grad Island (Prespa Lake, Macedonia, ~18 ha, 40°52'09"N, 20°59'17"E). Each year the area was intensively patrolled (2–12 observers). Overall, 169 search days enabled us to capture 1830 individuals. Among them, 466 could be aged at 1225 capture occasions. Every captured individual was sexed when sexually dimorphic, aged, and permanently marked using a notch-code on the marginal-scutes (Cagle, 1939). In the course of recaptures, age was re-estimated blindly (for error rate and more details on ageing and general CR methodology see Bonnet et al., 2016 and Arsovski et al., 2018).

Multievent model design

We performed goodness-of-fit tests on the datasets based on the CJS model. Attributed to the detection of trap dependence and transience (see Results) that might be induced either by age-specific variations of recapture and survival probability but also by capture heterogeneity (Olivier, 2002; Fichoux et al., 2014), we used multievent modelling (Pradel, 2005). Events are field observations masking possibly multiple states; multievent models estimate the probability of observing a state given the event it is masked under using hidden Markov chains. Accordingly, sex was coded as a state in order to deal with sex uncertainty in young individuals. In order to deal with potential heterogeneity in recapture rates, we built mixture models (Pledger, Pollock & Norris, 2003) in which individuals can belong to two classes of individuals exhibiting different recapture probabilities (see for instance Prévot-Julliard, Lebreton & Pradel, 1998 for such a procedure).

Our models were based on nine underlying biological states (Table 2), i.e. a combination of three variables: sex, site (Esquineau and Baïsses for European pond turtles; Plateau and Beach for Hermann's tortoises) and recapture heterogeneity class, and a dead state. At first capture, individuals depart from all states but dead. Subsequently, they can annually transit between

states following five successive transition matrices: survival from t to $t + 1$ (matrix Φ , Table 3a), dispersal between sites, given the individual survived (matrix Ψ , Table 3b), and change of recapture heterogeneity class given

Tableau 3 Elementary matrices describing transitions among elementary states ('m/M' and 'f/F' refer to males and females, respectively, capitals denoting high recapture probability and vice versa; '1' and '2' refer to the two sites of both datasets: Esquineau/the Plateau and Faïsses/the Beach, respectively; Table 2): (a) survival matrix Φ , ϕ is the probability to survive from t to $t + 1$; (b) dispersal matrix Ψ , w is the probability to stay faithful to the site of first capture from t to $t + 1$, whereas after a dispersal event the elementary state is prefixed a 'd' (e.g. M1 \rightarrow dM1); (c) change of heterogeneity class matrix F , f is the probability of reaching the high recapture probability class; (d) first event matrix P , p is the probability of being recaptured after which the departure state is prefixed a 'c', whereas when failed to be recaptured the prefix is '0'; (e) second event matrix S , s is the probability to assess the sex of the individual, 0 – unobserved, 1 – observed as male in Esquineau/on the Plateau, 2 – observed as female in Esquineau/on the Plateau, 3 – observed as unsexable in Esquineau/on the Plateau, 4 – observed as male in Faïsses/on the Beach, 5 – observed as female in Faïsses/on the Beach and 6 – observed as unsexable in Faïsses/on the Beach

(a) matrix Φ

	M1	m1	F1	f1	M2	m2	F2	f2	†
M1	ϕ	0	0	0	0	0	0	0	$1 - \phi$
m1	0	ϕ	0	0	0	0	0	0	$1 - \phi$
F1	0	0	ϕ	0	0	0	0	0	$1 - \phi$
f1	0	0	0	ϕ	0	0	0	0	$1 - \phi$
M2	0	0	0	0	ϕ	0	0	0	$1 - \phi$
m2	0	0	0	0	0	ϕ	0	0	$1 - \phi$
F2	0	0	0	0	0	0	ϕ	0	$1 - \phi$
f2	0	0	0	0	0	0	0	ϕ	$1 - \phi$
†	0	0	0	0	0	0	0	0	1

(b) matrix Ψ

	M1	m1	F1	f1	M2	m2	F2	f2	dM1	dm1	dF1	df1	dM2	dm2	dF2	df2	†
M1	ψ	0	0	0	0	0	0	0	$1 - \psi$	0	0	0	0	0	0	0	$1 - \phi$
m1	0	ψ	0	0	0	0	0	0	0	$1 - \psi$	0	0	0	0	0	0	$1 - \phi$
F1	0	0	ψ	0	0	0	0	0	0	0	$1 - \psi$	0	0	0	0	0	$1 - \phi$
f1	0	0	0	ψ	0	0	0	0	0	0	0	$1 - \psi$	0	0	0	0	$1 - \phi$
M2	0	0	0	0	ψ	0	0	0	0	0	0	0	$1 - \psi$	0	0	0	$1 - \phi$
m2	0	0	0	0	0	ψ	0	0	0	0	0	0	0	$1 - \psi$	0	0	$1 - \phi$
F2	0	0	0	0	0	0	ψ	0	0	0	0	0	0	0	$1 - \psi$	0	$1 - \phi$
f2	0	0	0	0	0	0	0	ψ	0	0	0	0	0	0	0	$1 - \psi$	$1 - \phi$
†	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

(c) matrix F

	M1	m1	F1	f1	M2	m2	F2	f2	†
M1	1	0	0	0	0	0	0	0	0
m1	0	1	0	0	0	0	0	0	0
F1	0	0	1	0	0	0	0	0	0
f1	0	0	0	1	0	0	0	0	0
M2	0	0	0	0	1	0	0	0	0
m2	0	0	0	0	0	1	0	0	0
F2	0	0	0	0	0	0	1	0	0
f2	0	0	0	0	0	0	0	1	0
dM1	0	0	0	0	f	$1 - f$	0	0	0
dm1	0	0	0	0	f	$1 - f$	0	0	0
dF1	0	0	0	0	0	0	f	$1 - f$	0
df1	0	0	0	0	0	0	f	$1 - f$	0
dM2	f	$1 - f$	0	0	0	0	0	0	0
dm2	f	$1 - f$	0	0	0	0	0	0	0
dF2	0	0	f	$1 - f$	0	0	0	0	0
df2	0	0	f	$1 - f$	0	0	0	0	0
†	0	0	0	0	0	0	0	0	1

Table 3 Continued.

(d) matrix P

	0M1	0m1	0F1	0f1	0M2	0m2	0F2	0f2	cM1	cm1	cF1	cf1	cM2	cm2	cF2	cf2	†
M1	$1-p$	0	0	0	0	0	0	0	p	0	0	0	0	0	0	0	0
m1	0	$1-p$	0	0	0	0	0	0	0	p	0	0	0	0	0	0	0
F1	0	0	$1-p$	0	0	0	0	0	0	0	p	0	0	0	0	0	0
f1	0	0	0	$1-p$	0	0	0	0	0	0	0	p	0	0	0	0	0
M2	0	0	0	0	$1-p$	0	0	0	0	0	0	0	p	0	0	0	0
m2	0	0	0	0	0	$1-p$	0	0	0	0	0	0	0	p	0	0	0
F2	0	0	0	0	0	0	$1-p$	0	0	0	0	0	0	0	p	0	0
f2	0	0	0	0	0	0	0	$1-p$	0	0	0	0	0	0	0	p	0
†	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

(e) matrix S

	0	1	2	3	4	5	6
0M1	1	0	0	0	0	0	0
0m1	1	0	0	0	0	0	0
0F1	1	0	0	0	0	0	0
0f1	1	0	0	0	0	0	0
0M2	1	0	0	0	0	0	0
0m2	1	0	0	0	0	0	0
0F2	1	0	0	0	0	0	0
0f2	1	0	0	0	0	0	0
cM1	0	s	0	$1-s$	0	0	0
cm1	0	s	0	$1-s$	0	0	0
cF1	0	0	s	$1-s$	0	0	0
cf1	0	0	s	$1-s$	0	0	0
cM2	0	0	0	0	s	0	$1-s$
cm2	0	0	0	0	s	0	$1-s$
cF2	0	0	0	0	0	s	$1-s$
cf2	0	0	0	0	0	s	$1-s$
†	1	0	0	0	0	0	0

the individual survived and changed site (matrix F, Table 3c). The approach was simpler on the Hermann's tortoises, not parameterizing matrices ψ and F since individuals did not change sites, nor were caught in traps. Note that for easier implementation, ψ is a 9·17 matrix where eight departure states can transit to a ‘stay’ or ‘moved’ state. F is thus a 17·9 matrix, that allows ‘moved’ individuals to change recapture probability class (since we suspect recapture heterogeneity to be related to trap location we assumed that ‘stay’ individuals would not change recapture heterogeneity class). Finally, individuals can be recaptured or not. For easier implementation, this event matrix was split into two matrices, one allowing to model recapture probability given the states (matrix P, Table 3d), the other to estimate the probability of correctly sexing individuals (matrix S, Table 3e).

Building biological scenarios

Since young and small European pond turtles are less mobile and therefore less likely to be captured in a trap, two age classes were considered when modelling recapture probability (additional explorations would require a bigger sample): neonate-to-2-year-olds and older than 2 years. Initially, survival-at-age was a linear covariate with a plateau at age six. The more numerous tortoise dataset allowed multiple combinations of age-recapture probability to be explored, while maintaining an age effect on survival. Subsequently, in both species we explored multiple additive relationships with age, site, sex, time and capture heterogeneity.

Afterwards, maintaining the best parametrization of recapture probabilities we explored the effects of sex and site on survival. Lastly, we explored different parametrizations of the age effect on survival probabilities, namely linear, logarithmic and quadratic versus discrete, and different age at plateau. We superimpose our results from the best-fit discrete model against those aided by covariates and note the possible benefits and drawbacks. All models were implemented in E-SURGE (Choquet, Rouan & Pradel, 2009) separately per species, ranking competitive models using Akaike information criteria (AIC, Burnham & Anderson, 2002).

Table 4 Breakdown of numbers of captured European pond turtles from Camargue, France and Hermann's tortoises from Golem Grad island, Macedonia per hatching-year

Hatching-year	European pond turtle	Hermann's tortoise
1990	3	/
1991	6	/
1992	11	/
1993	12	/
1994	18	/
1995	11	/
1996	4	/
1997	6	/
1998	16	/
1999	16	7
2000	16	10
2001	6	16
2002	4	14
2003	16	34
2004	26	36
2005	26	41
2006	28	44
2007	36	64
2008	15	87
2009	15	48
2010	4	12
2011	3	5
2012	/	19
2013	/	15
2014	/	7
2015	/	7

Results

All 298 European pond turtles had hatched between 1990 and 2011, and all 466 Hermann's tortoises between 1999 and 2015. The chronological breakdown of captured animal numbers per hatching year can be found in Table 4. In both data-sets the goodness-of-fit tests were significant ($\chi^2 = 127.35$ and 72.09 , d.f. = 60 and 31, respectively, $P < 0.001$) with significant transience and trap-dependence (both $P < 0.001$), suggesting strong survival or recapture heterogeneity.

European pond turtle

The best-fitted model (Table 5) implied an additive time variation of both age classes' recapture probabilities, the second (>2 years old) also exhibiting heterogeneity and sex differences. Removing the effect of recapture heterogeneity increases AIC sharply (by 82.6), confirming its importance. The younger age-class displayed similar capture probabilities as the low heterogeneity class of the older age class (on average ranging between 0.23 and 0.34, between capture occasions). Higher heterogeneity class males were consistently higher than the respective females, with average respective estimates of 0.84 and 0.72. Survival retained the linear age-effect and did not vary between sites and sexes. Exploring a survival age-plateau resulted with two very

close models (DAIC = 0.36), with survival summing at 4 and 5 years of age. Nevertheless, neonate survival estimates are significantly different (0.10 ± 0.05 vs. 0.20 ± 0.07); the discrete model was unable to provide these estimates due to a lack of neonates. All three models demonstrate a steep increase in survival probability between zero and 4 years of age (Fig. 1). The differences in survival probabilities between the discrete and covariate models were low, ranging between one and nine percent among age-classes. Nevertheless, the discrete model was much less precise (Fig. 1).

Hermann's tortoise

After model selection, regarding recapture probability 1- to 5-year-olds formed a separate cohort whereas all further age classes were considered separately. All are site dependent, while only those from the Plateau experience recapture heterogeneity (lowering AIC by 71). Among them, the higher heterogeneity class ranged between 0.56 and 0.71, the low

heterogeneity class from 0.01 to 0.07 and Beach tortoises somewhere in the middle between 0.32 and 0.40. All exhibit additive time variation. Exploring different parameterizations of the age-effect on survival resulted with a logarithmic to linear relationship reaching a plateau at 4–6 years of age, or a discrete model summing at the age of four [DAIC between these models ranged between 0.6 and 1.3, Table 5; models whose DAIC from the best fit model ≤ 2 are considered to also have substantial support (Burnham & Anderson, 2002)]. Despite lowering AIC, adding site and/or sex effects on discrete model survival failed to provide precise estimates, thus the age-effect discrete model was used for comparison purposes. With covariates, best model fit was achieved when female survival from the Plateau was considered separately. Plateau female survival probabilities increased linearly with age from 0.08 when neonate to 0.86 when 5-years-old. Conversely, male tortoises and females from the Beach expressed significantly higher survival at all ages starting at 0.32 with a plateau at 0.97 (Fig. 2). Superimposing the discrete model estimates (despite being slightly lower due to lack of separation of Plateau females) showed a broad overlap of confidence intervals but was unable to estimate neonate ($N = 1$) survival (Fig. 2).

Discussion

By means of advanced multievent CR modelling, this study demonstrates that even sparse datasets can be used to obtain age-specific estimates of survival in long-lived species. Consequently, it demonstrates that, as in other long-lived vertebrates, the substantially prolonged immature phase of both the Hermann's tortoise and the European pond turtle entail a steep and progressive increase in survival with age.

The age-linear covariate (continuous) models are streamlined versions of their discrete counterparts, suggesting no bias in the age-specific survival estimates. Moreover, the continuous models clearly outperformed the discrete models in terms of precision, especially in the sparser dataset of the European

r	Model definition		k	Dev.	AIC	w
	Survival	Recapture				
European pond turtle						
12	Lin_6*sex*site	[age ≤ 2*site; age > 2*H*site*sex] + year	44	2608.0	2696.0	0.0
17	Lin_6*sex*site	[age ≤ 2*H; age > 2* H*site*sex] + year	44	2610.1	2698.1	0.0
13	Lin_6*sex*site	[age ≤ 2; age > 2*H*site*sex] + year	43	2610.6	2696.6	0.0
21	Lin_6*sex*site	age ≤ 2; age > 2*H*site*sex	29	2647.0	2705.0	0.0
23	Lin_6*sex*site	[age ≤ 2; age > 2*site*sex] + year	35	2708.5	2778.5	0.0
14	Lin_6*sex*site	[age ≤ 2; age > 2*H*site] + year	39	2619.0	2697.0	0.0
11	Lin_6*sex*site	[age ≤ 2; age > 2*H*sex] + year	39	2617.9	2696.0	0.0
15	Lin_6*sex*site	[age ≤ 2; age > 2*H] + year	37	2623.5	2697.5	0.0
8	Lin_6*sex	[age ≤ 2; age > 2*H*sex] + year	37	2618.5	2692.5	0.0
6	Lin_6*site	[age ≤ 2; age > 2*H*sex] + year	37	2618.4	2692.4	0.0
5	Lin_6	[age ≤ 2; age > 2*H*sex] + year	36	2618.7	2690.7	0.1
4	Log_6	[age ≤ 2; age > 2*H*sex] + year	36	2618.6	2690.6	0.1
22	Quad_6	[age ≤ 2; age > 2*H*sex] + year	36	2633.7	2705.7	0.0
1	Lin_5	[age ≤ 2; age > 2*H*sex] + year	36	2614.7	2686.7	0.4
3	Log_5	[age ≤ 2; age > 2*H*sex] + year	36	2618.0	2690.0	0.1
19	Quad_5	[age ≤ 2; age > 2*H*sex] + year	36	2629.7	2701.7	0.0
2	Lin_4	[age ≤ 2; age > 2*H*sex] + year	36	2615.1	2687.1	0.3
9	Log_4	[age ≤ 2; age > 2*H*sex] + year	36	2621.2	2693.2	0.0
18	Quad_4	[age ≤ 2; age > 2*H*sex] + year	36	2626.1	2698.1	0.0
16	Lin_3	[age ≤ 2; age > 2*H*sex] + year	36	2625.6	2697.6	0.0
20	Log_3	[age ≤ 2; age > 2*H*sex] + year	36	2631.7	2703.7	0.0
10	Quad_3	[age ≤ 2; age > 2*H*sex] + year	36	2623.7	2695.7	0.0
7	Age	[age ≤ 2; age > 2*H*sex] + year	41	2609.3	2691.3	0.0
Hermann's tortoise						
53	Age	age	33	4360.2	4426.2	0.0
43	Age	age*year	155	3966.0	4276.0	0.0
37	Age	age + year	48	4015.5	4111.5	0.0
57	Age	[age0; 1–9] + year	32	4510.6	4574.6	0.0
55	Age	[age0; 1;2–9] + year	34	4473.1	4541.1	0.0
54	Age	[age0; 1–2;3–9] + year	34	4412.3	4480.3	0.0
51	Age	[age0; 1–3;4–9] + year	34	4345.2	4413.2	0.0
50	Age	[age0; 1–4;5–9] + year	34	4290.1	4358.1	0.0
48	Age	[age0; 1–5;6–9] + year	34	4227.1	4295.1	0.0
41	Age	[age0; 1–6;7–9] + year	34	4160.3	4228.3	0.0
40	Age	[age0; 1–7;8–9] + year	34	4156.8	4224.8	0.0
42	Age	[age0; 1–8;9] + year	34	4193.6	4261.6	0.0
36	Age	[age0; 1–3;4;5;6;7;8;9] + year	46	4019.2	4111.2	0.0
46	Age	[age0; 1–2;3–5;6–9] + year	36	4223.0	4295.0	0.0
52	Age	[age0; 1;2;3;4–9] + year	38	4341.2	4417.2	0.0
45	Age	[age0; 1;2–3;4–5;6–9] + year	38	4213.0	4289.0	0.0
47	Age	[age0; 1–2;3–5;6–9] + year	36	4223.0	4295.0	0.0
49	Age	[age0; 1–5;6–9] + year	34	4227.1	4295.1	0.0
56	Age	[age0; 1;2;3–9] + year	34	4473.1	4541.1	0.0
38	Age	[age0; 1–5;6;7;8;9] + year	40	4033.5	4113.5	0.0
44	Age	[age0; 1–3;4–5;6–9] + year	36	4216.7	4288.7	0.0
39	Age	[age0; (1–5;6;7;8;9)*sex] + year	45	4029.7	4119.7	0.0
29	Age	[age0; (1–5;6;7;8;9)*site] + year	45	3947.7	4037.7	0.0
31	Age	[age0; (1–5;6;7;8;9)*H] + year	50	3942.5	4042.5	0.0
30	Age	[age0; (1–5;6;7;8;9)*site*H] + year	60	3920.1	4040.1	0.0
25	Age	[age0; (1–5;6;7;8;9)*site(P*H)] + year	53	3926.6	4032.6	0.0
33	Age	[age0; (1–5;6;7;8;9)*sex*site*H] + year	80	3899.4	4059.4	0.0
35	Age	[age0; 1–5;(6;7;8;9)*site(P*H)] + year	51	3997.0	4099.0	0.0

Table 5 Model selection procedure showing all competing models for both species in order of conception: r = model rank; k = number of parameters; Dev. = residual deviance; AICc = Akaike information criteria; w = AICc relative weight; age = discrete model; H = capture heterogeneity; P = Plateau; Lin, Quad; Log = linear, quadratic, logarithmic covariate, respectively, on the age-survival relationship; _ = survivalplateau

Table 5 Continued.

r	Model definition		k	Dev.	AIC	w
	Survival	Recapture				
28	Lin	[age0; (1-5;6;7;8;9)*site(P*H)] + year	47	3943.6	4037.6	0.0
34	Quad	[age0; (1-5;6;7;8;9)*site(P*H)] + year	47	3973.9	4067.9	0.0
21	Log	[age0; (1-5;6;7;8;9)*site(P*H)] + year	47	3936.9	4030.9	0.0
24	Age_8	[age0; (1-5;6;7;8;9)*site(P*H)] + year	52	3928.3	32.3	0.0
2	Lin_8	[age0; (1-5;6;7;8;9)*site(P*H)] + year	46	3940.8	4032.8	0.0
16	Log_8	[age0; (1-5;6;7;8;9)*site(P*H)] + year	46	3935.9	4027.9	0.0
19	Age_7	[age0; (1-5;6;7;8;9)*site(P*H)] + year	51	3928.5	4030.5	0.0
20	Lin_7	[age0; (1-5;6;7;8;9)*site(P*H)] + year	46	3938.5	4030.5	0.0
13	Log_7	[age0; (1-5;6;7;8;9)*site(P*H)] + year	46	3935.0	4027.0	0.0
18	Age_6	[age0; (1-5;6;7;8;9)*site(P*H)] + year	50	3930.1	4030.1	0.0
22	Lin_6	[age0; (1-5;6;7;8;9)*site(P*H)] + year	46	3939.1	4031.1	0.0
10	Log_6	[age0; (1-5;6;7;8;9)*site(P*H)] + year	46	3934.7	4026.7	0.0
17	Age_5	[age0; (1-5;6;7;8;9)*site(P*H)] + year	49	3930.3	4028.3	0.0
12	Lin_5	[age0; (1-5;6;7;8;9)*site(P*H)] + year	46	3934.9	4026.9	0.0
7	Log_5	[age0; (1-5;6;7;8;9)*site(P*H)] + year	46	3933.6	4025.6	0.0
9	Age_4	[age0; (1-5;6;7;8;9)*site(P*H)] + year	48	3930.3	4026.3	0.0
23	Lin_4	[age0; (1-5;6;7;8;9)*site(P*H)] + year	46	3939.5	4031.5	0.0
8	Log_4	[age0; (1-5;6;7;8;9)*site(P*H)] + year	46	3934.2	4026.2	0.0
14	Age_3	[age0; (1-5;6;7;8;9)*site(P*H)] + year	47	3933.2	4027.2	0.0
32	Lin_3	[age0; (1-5;6;7;8;9)*site(P*H)] + year	46	3961.0	4053.0	0.0
27	Log_3	[age0; (1-5;6;7;8;9)*site(P*H)] + year	46	3941.9	4033.9	0.0
2	Age_4*site	[age0; (1-5;6;7;8;9)*site(P*H)] + year	52	3912.9	4016.9	0.2
5	Log_5*site	[age0; (1-5;6;7;8;9)*site(P*H)] + year	47	3925.2	4019.2	0.1
15	Age_4*sex	[age0; (1-5;6;7;8;9)*site(P*H)] + year	52	3923.6	4027.6	0.0
6	Log_5*sex	[age0; (1-5;6;7;8;9)*site(P*H)] + year	47	3925.2	4022.9	0.0
11	Age_4*sex*site	[age0; (1-5;6;7;8;9)*site(P*H)] + year	60	3906.8	4026.8	0.0
4	Log_5*sex*site	[age0; (1-5;6;7;8;9)*site(P*H)] + year	49	3920.8	4018.8	0.1
3	Age_4*site(P*sex)	[age0; (1-5;6;7;8;9)*site(P*H)] + year	52	3914.0	4018.0	0.1
1	Log_5*site(P*sex)	[age0; (1-5;6;7;8;9)*site(P*H)] + year	47	3921.2	4015.2	0.5

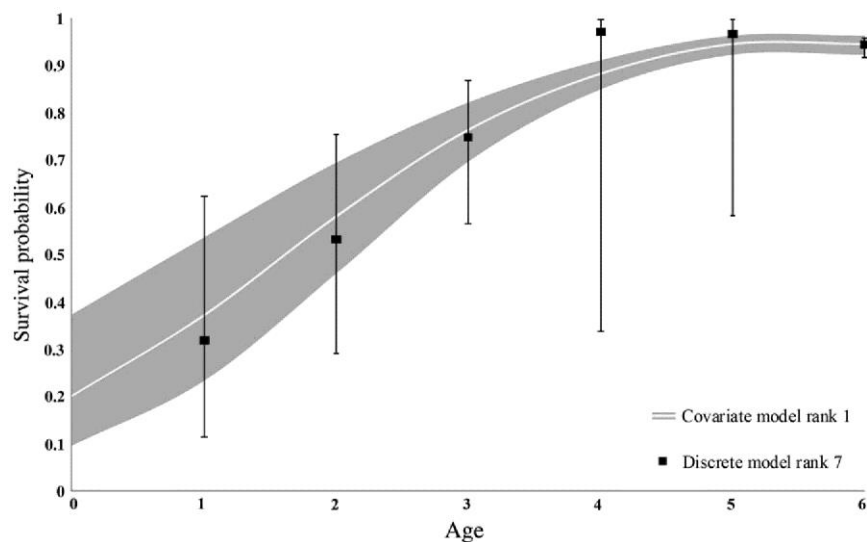


Figure 1 Estimated age-specific mean survival probabilities and 95% CIs of young European pond turtles from Camargue, France obtained from a discrete model (Model rank 7, Table 5), superimposed against the estimates and 95% confidence spread of mean age-specific survival probabilities of the same population obtained from the best-fit covariate model (Model rank 1, Table 5).

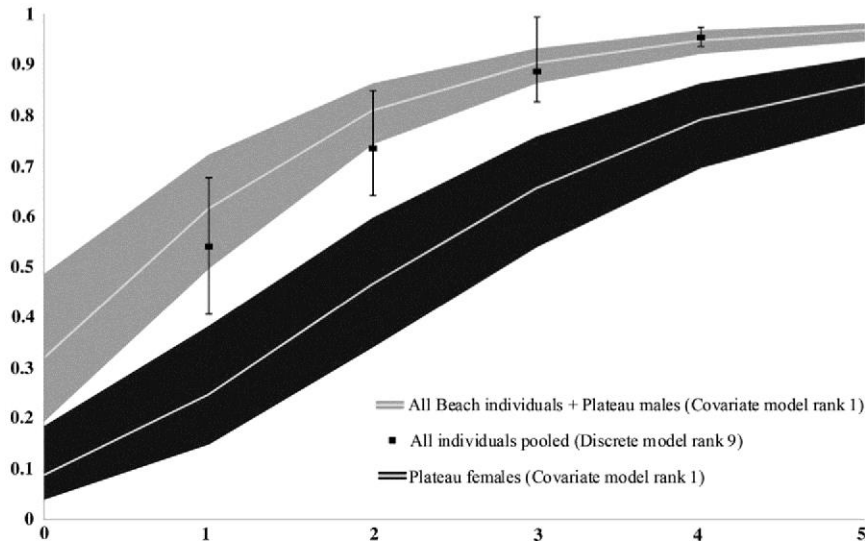


Figure 2 Estimated age-specific mean survival probabilities and 95% CIs of young Hermann's tortoises from Golem Grad Island, Macedonia obtained from a discrete model (Model rank 9, Table 5), superimposed against the estimates and 95% confidence spread of mean age-specific survival probabilities of two separate cohorts (females from the Plateau, and both sexes from the Beach along with males from the Plateau) from the same population obtained from the best-fit covariate model (Model rank 1, Table 5).

pond turtle (Fig. 1). Most notably, the discrete models failed to estimate neonate survival due to the lack of marked neonates. The continuous models partially solve this issue by projecting the linear relationship of age and survival on neonate survival. Nevertheless, such predictions bear considerable uncertainty and should only be considered surrogates until they can be supported by proper data collected on this age class. Attributed to the difficulty of capturing and recapturing elusive immature reptiles, researchers have often opted for indirect estimates of juvenile survival, such as catch-curve analyses (Table 1), or indirect mathematical approaches (Pike et al., 2008). The only robust study comes from a reintroduction program of western Hermann's tortoise adults allowing for all future recruits to be monitored – an exceptional case providing 19 years of data and precise discrete estimates (Fernández-Chacón et al., 2011); superimposing our eastern subspecies estimates reveals no differences between the taxa, and simply corroborates the idea that age-linear covariates helps streamline results without added bias. The following results thus seem encouraging; ultimately, substantial field effort followed by appropriate statistical approaches can provide precise trait estimates, indispensable to matrix models underlying evolutionary ecology research, and efficient conservation policies.

Our results seemingly conform to existing literature (Table 1) – mean survival is lowest in neonates, yet never below 20%, and it increases progressively with age (Fig. 1 and 2). Mitrus (2005) estimated surprisingly low survival values for neonate European pond turtles (0.11); whilst this might reflect the true situation, the author provides “minimal annual survivorships (numbers recaptured/number captured in previous year)”, thus in practice actually describing a mix between survival and recapture rates. The age-survival relationships do not vary between our studied species despite their ecological differences and distant phylogenetic relatedness, possibly alluding a similar trend throughout this diverse clade (183 species in Crawford et al., 2014). Furthermore, several other long-lived vertebrates also exhibit a linear increase in age-specific survival (see for instance DeLong et al., 2017; Forslund & Pärtel, 1995; Jorgenson et al., 1997; Schwarz & Stobo, 2000; Shine & Charnov, 1992). Different species reach their respective survival plateaus at different ages, often corresponding with maturity [2–3 years in bighorn sheep (Jorgenson et al., 1997 note that first reproduction usually occurs later), 4 years in grey seals (Schwarz & Stobo, 2000), 7 years in Steller sea lions (Hastings et al., 2011), 5 years in California sea lions (DeLong et al., 2017)]. Both Hermann's tortoises and European pond turtles reach maturity between the ages of eight and 12 (six in Olivier, 2002; Rogner, 2009; Bertolero et al., 2011), yet arrive at a survival plateau earlier - at approximately four- to 5-years-old (Fig. 1 and 2). This is likely a consequence of the final hardening of the carapace, which can bring obvious survival benefits prior maturity (Wilbur & Morin, 1988). After maturity, European pond turtles from Camargue experience sex differences in survival (Olivier et al., 2010); nonetheless, our results overrule the possibility of it originating prior maturity. When immature neither species is obviously sexually dimorphic (Rogner, 2009; Bertolero et al., 2011), thus sex-specific habits or environmental pressures (e.g. sexual coercion in the Hermann's tortoise (Hailey & Willemsen, 1999)) that could influence survival prior maturity are either elusive, or likely not present. In adult Hermann's tortoises sex-specific survival is not common apart from few populations with a bias in sex-ratio (Hailey & Willemsen, 1999). Interestingly, the Golem Grad tortoise population has the highest reported bias in sex-ratio of this species, reaching its maximum on the Plateau where only 5% of all adult individuals are female (Bonnet et al., 2016). Our best-fit model implies significantly lower survival of younger females from this locality from birth (Fig. 2). We hypothesize this result to be a consequence of male coercion on the oldest females in our dataset, later projected onto the youngest age classes by the covariate. As such, this example is also a cautionary message on the use of covariates! Nevertheless, adult survival insight is needed, and more data for the discrete

model to confirm these claims. Pin-pointing the age at which Plateau females are initially affected should be explored, but is beyond the scope of the current study.

The high variation in juvenile survival estimates that fail to give age- or at least stage-specific estimates in Table 1 is likely owed to the age-class that was predominant in the respective datasets. This mandates prudence when interpreting them in an evolutionary-ecological framework or applying them to conservation policies. Our results corroborate that immature survival increases with age in long-lived species, additionally suggesting it occurs rather steeply in chelonians. This is likely a consequence of ontogenic shifts in morphology, physiology and behaviour and therefore alterations in interactions with the environment (Golubović, 2015). It would come as a surprise if shifts in age-specific survival do not translate to age-specific shifts in other aspect of a species' life history. Indeed, after the age of five Golem Grad tortoises experience ever-increasing age-specific body size variation (Fig. 1, Arsovski et al., 2018). Armed with a hard carapace they can reach a survival plateau and therefore enough confidence to start expressing individuality in their respective environments; interestingly, our models' preference to consider tortoise capture probabilities independently per age after the age of five corroborates this notion. Remarkably, behavioural shifts might follow this trend as well: Hermann's tortoises alter their antipredator behaviours after maturity (Golubović, 2015). We suggest that future early life studies on species with a long immature phase should focus on age-specific considerations of other aspects of animals' life histories.

Conclusion

Reliable projection matrices based on accurate early life agespecific survival estimates are essential for fundamental and conservation purposes. We suggest a simple way of facilitating the process of obtaining these estimates even with sparse datasets. Systematic approaches to survey young animals should be unified, and the resulting (even sparse) age-specific sets of data can usefully be modelled using advanced statistical techniques. Continuous annual surveys of small and elusive animals might seem as an inefficient allocation of labour considering the output, but hopefully the advancements in direct methodological approaches will gradually change this notion.

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