

**RUN-OF-THE-MILL ECOLOGY
TO SEXUAL BRUTALITY AND
EVOLUTION: ANNALS OF AN
AROUSED TORTOISE
POPULATION**





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ABSTRACT

The following story offers a humble example of islands as natural laboratories, stressing the significance of insights gained from free-ranging animals in a somewhat simplified context. Two generous data-sharing populations of promiscuous sexually coercive Hermann's tortoises (*Testudo hermanni*, a species with delayed maturity [~ 10 years]) from the Prespa Lake Region in Macedonia were scrutinized. Comparisons between island (Golem Grad, divided into narrow shores and a large plateau) and mainland (Konjsko) populations revealed age-specific life-history trends and behavioural peculiarities. The island context brought to attention very unusual demographic processes, eventually resonating with a seemingly inevitable population doom brought upon by insufferable sexual conflict.

Neonates to three-year old tortoises exhibit slow growth and low variation in body size (VBS) among individuals, likely illustrating the impact of a soft shell and lack of parental care. The subsequent gradual approach of a survival plateau (annual survival rate increase: 0.30 to 0.70) parallels a gradual increase in confidence and a slowly hardening shell that promotes better foraging capabilities reflected onto a phase of fast linear growth. Unlike long-lived mammals that are in a hurry to reach maturity at a certain size (lowering VBS) that will increase survival and ensure reproduction during a non-growing adult phase, tortoises have the potential for indeterminate growth (estimated individual asymptotic sizes from incremental growth after maturity on Golem Grad range from ~ 153 to ~ 224). When protected by a hard carapace that translates into a survival plateau (0.90) at the age of five, indeterminate growth leaves room for young tortoises to express individuality in growth regimes, promoting an ever increasing VBS prior to adulthood. Size-at-maturity is thus a blurred notion in these tortoises. Testosterone levels and sexual activity indicate that minimal size at maturity in precocious males is somewhere between 115-120mm straight carapace length (SCL), whereas VBS and literature point to a range of 140-150mm. Clearly some tortoises mature early, while others are in no

rush at all. Sexual size dimorphism in the *Testudo* genus suggests most larger-at-maturity tortoises are likely females; Golem Grad population-mean female asymptotic size estimates make no exception.

Nevertheless, actual body sizes on the island do not reflect estimates from incremental growth – the largest individuals are males. At ~100 individuals/ha with an operational sex ratio (OSR [$\sigma/\text{♀}$]) of ~11, male sexual coercion from constantly aroused tortoises drastically increased female mating costs, wreaking havoc on Golem Grad. Adult survival estimates are considerably higher in males (0.97) than in females (0.84). This is accompanied with low female body-condition, intense cloacal injuries inflicted by males, that can even push females from the island's high cliffs. Overall, island females do not live long and are also discouraged from reproduction (dissections data). Even implementing species' average fecundity, simulations predict recruitment insufficiency and a decline in the number of females, exacerbating OSR-bias. Tortoises are long-lived animals; adult cohorts ensure population growth despite environmental fluctuations. Nevertheless, on the island the temporal-variance of adult female survival has succumbed to the pressure stirred up by male sexual coercion and will likely lead to population extinction. Perhaps most surprisingly, cloacal injuries indicate that even immature females (~8 years old) have become the target of the maladaptive sexual appetite of males. After reaching nine years, females that inhabit the island's macho Plateau (only 5% of adults are females) are harassed and exhibit lower average annual survival probabilities.

This unfortunate demographic drift does not seem to be the only consequence of OSR bias and high density – island frustrated males court and mount other males more frequently than females. They even exhibit extravagant sexual behaviours, attempting to copulate with dead conspecifics, empty shells, and stones. Golem Grad tortoises elucidated the first natural example of a “prison effect,” whereby a high population density combined with female deprivation (but not accompanied with abnormal testosterone levels) triggered same-sex sexual behaviours (SSB) as a mere outlet of sexual stimulation. More generally, this supports the hypothesis that SSB can be a nonadaptive consequence of unusual proximate factors rather than reflecting physiological

disorders. Finally, SSB may even benefit females by diluting aggressive male mounting efforts among males as well.

In light of the expensive conservation endeavours on the endangered Hermann's tortoises in western Europe, life-history insight gained from Golem Grad tortoises can provide a valuable conservation lesson: taking into account Hermann's tortoises' environmental sex determination, captive breeding programs can easily create dense female biased colonies that will stand the best chance of creating a prosperous breeding population in the shortest time. Such valuable advice can reduce conservation costs, and help reverse the artificial separation of fundamental research from conservation, particularly evident in the developing (e.g. Macedonia) and third world. After all, applied conservation should only be the inevitable and likely unavoidable side-effect of research, rather than a short term must!

Une dérive de la vie de tous les jours vers la brutalité sexuelle : chroniques d'une population de tortues surexcitées

Ce manuscrit illustre modestement en quoi les îles sont des laboratoires naturels utiles à la recherche grâce à leur nature simplifiée. Deux populations de tortues d'Hermann (*Testudo hermanni*) nous ont fourni des données denses sur la démographie et les comportements d'un organisme à maturité sexuelle tardive (~10 ans) et au système d'appariement coercitif. Dans la région du lac Prespa en Macédoine, nous avons comparé une population insulaire (Golem Grad, avec des rivages étroits et un plateau) avec une population continentale (Konjsko). Les analyses des variations des traits d'histoire de vie au cours de la croissance et selon le sexe ont révélé des surprises. Dans le contexte insulaire, une dérive démographique causée par les comportements sexuels des mâles conduit la population vers l'extinction ; il s'agit du premier cas décrit en conditions naturelles.

De la naissance jusqu'à l'âge de trois ans, les tortues grandissent lentement et au même rythme, probablement à cause de l'absence de soins parentaux et de la faible protection de la petite carapace qui canalisent les variations. Ensuite, la valeur protectrice de la carapace augmente, ce qui ouvre différentes options alimentaires, accompagnées par une accélération de la croissance et de la survie (de 0.3 à 0.7). Contrairement aux mammifères qui sont sous forte pression pour atteindre le plus vite possible la maturité, ce qui brime les variations interindividuelles de croissance et de taille, les jeunes tortues qui peuvent grandir toute leur vie expriment davantage de variations. Les estimations de taille asymptotique calculées grâce aux nombreuses recaptures au cours des années s'étalent alors de 154mm à 224mm pour la longueur. Une fois les tortues protégées par une solide carapace, dès 5 ans, les taux de survie plafonnent à des valeurs élevées (0.9). La très longue croissance continue laisse alors la place pour de multiples trajectoires, ce qui amplifie encore les divergences interindividuelles

avant et après la maturité. L'existence d'une taille exacte à maturité est une notion floue chez cette espèce. D'ailleurs, les taux de testostérone et d'activité sexuelle montrent que la maturité des individus précoces oscille entre 115mm et 120mm alors que la littérature propose 140mm à 150mm. Cet écart s'explique par le fait que certaines tortues deviennent adultes tôt tandis que d'autres non.

Dans le genre *Testudo*, le dimorphisme sexuel de taille penche vers les femelles; les estimations de taille asymptotique moyenne de nos deux populations sont conformes à cette règle. Les femelles sont plus grandes que les mâles à Konjsko, mais pas sur Golem Grad. Un processus doit empêcher les femelles insulaires de grandir pleinement.

Sur Golem Grad, avec environ 100 individus/ha et un sexe ratio opérationnel fortement biaisé (OSR : ♂/♀ ~11), les mâles harcassent les femelles continuellement et créent des ravages dans la population. La survie des mâles adultes est élevée (0.97) alors que celle des femelles est anormalement basse (0.84). Les femelles sont amaigries, souffrent de blessures cloacales, et sont même précipitées des falaises par les mâles surexcités. Sur l'île les femelles ne vivent pas longtemps et n'arrivent pas assez souvent à produire des œufs (données de dissection). Même en implémentant une fécondité moyenne pour l'espèce dans les modèles, les simulations prédisent un recrutement trop faible, un déclin du nombre de femelles, ce qui induit un cercle vicieux en exagérant le biais du sexe ratio et le taux d'harcèlement.

Les tortues sont des animaux longévifs, la stabilité des paramètres démographiques des cohortes adultes assure la viabilité des populations en dépit de fluctuations environnementales. Mais sur l'île, la variance temporelle de la survie des femelles adultes est fortement secouée par les assauts des mâles, ce qui peut entraîner l'extinction de la population. Cette violence comportementale touche même les immatures (~8 ans) qui victimes de l'appétit sexuel et mal dirigé des mâles montrent des blessures cloacales. La survie des femelles de plus de neuf ans, cernées par les mâles (5% de femelles adultes sur le plateau), décroît.

Cette dérive démographique, conséquence d'une forte densité combinée à un fort biais du sexe ratio, entraîne aussi une forte expression de comportements homosexuels parmi les mâles frustrés. Ces derniers montrent des comportements

sexuels exubérants, ils montent des cadavres de tortues, des carapaces vides, des pierres. Golem Grad apporte le premier exemple de "l'effet prison" en conditions naturelles, où une forte densité de population associée à un manque de partenaires sexuels déclenche de nombreux comportements homosexuels, exutoires d'une tension sexuelle, indépendamment d'une quelconque anomalie hormonale. D'une façon globale, ces résultats étayent l'hypothèse non-adaptative des comportements homosexuels comme simple conséquence de facteur proximaux sans impliquer de désordres physiologique. Peut-être que ces comportements homosexuels épargnent aussi les femelles.

Compte tenu des efforts à fournir pour préserver les populations de tortues d'Hermann qui sont menacées en Europe occidentale, nos résultats pourraient être utiles. Grâce à la détermination par la température d'incubation du sexe des tortues d'Hermann, des programmes d'élevage pourraient livrer de grandes quantités de femelles pour repeupler les populations fragilisées en limitant les coûts infligés par les mâles. Cette approche permettrait de réduire les coûts logistiques. Elle montre aussi la perméabilité entre les approches fondamentales et pratiques de la conservation ; notion qu'il faut injecter dans les pays en voie de développement (e.g. Macédoine). La conservation appliquée devrait d'ailleurs être considérée comme une production naturelle de la recherche.

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Islands act as a binding agent of the diverse subject matters this thesis deals with, and I can draw a strong parallel between the diversity of written subject matters and the diverse nature of the benefits I have acquired from one island in particular, Golem Grad in Prespa Lake, Macedonia. Thus, I would like to primarily express my most honest gratitude to its existence, for neither this PhD as the current crown of my biological knowledge would've materialized, nor a significant portion of my emotional personal connections that have moulded me in the human I am now.

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Last but surely not least, some of the “controversial” subjects of this thesis attracted media coverage, which I appreciate, but am not always the fondest of. Nevertheless, facilitated by such coverage, what I can only believe to be a product of serendipity took place – I met my partner. Ivo Kunovski thank you for being the most humble, loving person I have ever met and thank you for loving me with such intensity. I cannot anymore imagine my life prior to meeting you, and I cannot imagine my future life without you. I have never felt a bigger quantity of condensed love in the amount of time we have spent living together and apart, and I cannot wait to experience the love that life has in store for us.

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The entire manuscript follows the general form of a classical scientific paper in order to avoid the approach of simply piling together published papers, in a more or less artificial manner. From the very beginning, a common denominator (islands) was chosen to act as a binding agent, compiling the diverse published and unpublished material of this doctoral thesis into a singular product with a (hopefully) natural flow. The introductory chapter named "Islands as vectors of insight" announces a dichotomy which will resonate throughout the manuscript. This is most evident in the discussion, which has been split into three chapters. The first two ("run-of-the-mill ecology: islands as facilitators of biological insight enquiry" and "from run-of-the-mill to out-of-the-way: islands as vectors of peculiarities and mediators of applied research") parallel the introduced dichotomy, and are followed by a seemingly detached chapter on the conservation of the used model system. I hope to have overcome this detachment in the final segment ("broad reflection & relevance") where I briefly reflect on all presented and discussed results and attempt to melt them into an argument against the artificial separation of conservation from fundamental research.

1. ISLANDS AS VECTORS OF INSIGHT



“The environment is a kind of container, and life is like a liquid that adapts to fill it” (Clancy 2017); “current biodiversity seems to simply be the consequence of a collection of fortuitous events that have fallen victims to a plethora of evolutionary processes”. These are two statements that, prior to writing this thesis I believed summarize in a very broad sense the subject matter of the written word to follow. At present day perspective these sentiments not only sum up my subject matter in a broad sense, but perhaps the entire field of evolutionary biology, ‘and then some’. I find them nonetheless true and fitting, since they simplify very complicated concepts, and additionally, since I believe every endeavour can benefit from fortuity, particularly serendipitous fortuity.

Studying the product of fortuity would itself require a collection of fortuitous events, thus simplification opportunities are welcome. Isolated geographical areas i.e. islands in the broad sense (e.g. lakes are considered terrestrial analogues to islands [Fryer 1996]) offer exactly that. Going back to the first statement, if we imagine the environment to be a kind of container than we can imagine islands to be very well disjointed segments of that container sustaining fewer ‘liquids’ than the rest. The potential implications that come with this scenario offer extraordinary opportunities to gain:

- thorough insight on the isolated island inhabitants thanks to the lack of certain confounding factors and contingencies (‘fewer liquids’) i.e. *islands as facilitators of (run-of-the-mill) biological insight enquiry*, or
- some details of the peculiarities (flukes and quirks; fortuitous events themselves) that often arise from the exposure to disjointed-area-specific factors that due to their simplicity and isolation can perhaps lack factors of stabilization i.e. *islands as vectors of peculiarities*.

The former can be very beneficial, getting us closer to the identification of general laws in ecology and sometimes their general extrapolation (Lawton 1999), whereas the second one is overwhelmingly exciting since it offers a glimpse at the potential that has been hidden and overlooked in open environments. While extrapolation can obviously be immensely beneficial, such as in the context of efficient conservation policies and programs, unique peculiarities (while not necessarily easy to extrapolate) are some of the facets of the variation necessary

to sustain diversity and evolution. After all, if such variation is fortuitously better adapted to an ever-changing environment, it can morph into the new consistent phenotype. Witnessing (i.e. capturing instances of fortuity) is, in my opinion, the closest a biologist can come to the broadly used, but in my book controversial term - a blessing. During the following work I will make an attempt at unravelling the broadness of the preceding statements into examples from literature, details from my team's own work and finally a conclusion. Though any example can be perceived as underwhelming superimposed against seemingly endless variation, we know of no better way of untangling it.

While running the risk of adding a strong taste of cliché to this thesis, any subject combining islands, biodiversity, ecology and evolution cannot be approached without mentioning the Galapagos Archipelago, Charles Darwin or at least Rosemary and Peter Grant. While Darwin was the first to formally pioneer the idea of evolution through natural selection (Darwin 1859), the Grants have managed to capture some of the processes underlying natural selection in exhaustive work (from genetics to ecology) dealing with the 14 species of Galapagos finches (Grant & Grant 2003). During their four decades-long work they have explicitly demonstrated how the environment is like a container ('box' in their words) that finches continuously try to adapt to. The word 'continuously' is crucial in this context since in the past 2-5 million years that finches have been inhabiting the archipelago, the islands' environments have changed dramatically. Not only have droughts and wet seasons interchanged repeatedly, moulding the environment, but also due to their volcanic origin new islands have formed and old ones have shrunk or sank. Thus, not only is life like a liquid, but the containers are not completely solid either. The Galapagos Islands are still changing very rapidly and the Grants (2003) have captured fortuitous moments of dispersal and speciation within and between islands and have been able to follow these processes throughout. Witnessing the first settlers of a population of a species previously only present as a vagrant on an island, and subsequently monitoring each coming generation (Grant et al. 2001) while also monitoring cohabitants and environmental parameters likely falls more so in the ballpark of serendipity. I believe a 2006

report (Grant & Grant 2006) on the finches of the small Galapagos island of Daphne major to epitomize this occurrence, exemplifying both character release and character displacement phenomena. The former is hypothesized to have pushed the medium ground finch (*Geospiza fortis*) into exploiting the locally abundant small seeds by evolving smaller beak sizes (smaller seeds are preferred when abundant due to a tradeoff in the energetic rewards between feeding on small and large seeds [Benkman 1987]) in the absence of the smaller ground finch that would otherwise compete for that resource. Nevertheless, larger seeds were still present sustaining some larger *G. fortis* individuals among the smaller ones. A drought in 1977 caused a scarcity in small seeds, favouring large finch survival and decimating the numbers of smaller ones. A subsequent El Niño event brought plentiful rainfall renewing small and large seedbanks on the island, but also creating favourable conditions for the occasional vagrant large ground finches (*Geospiza magnirostris*) to stay and breed (two females and three males in 1982). Character displacement did not become evident while large seeds were abundant, but once another drought took place in 2004, the then plentiful *G. magnirostris*, which is much better adapted at exploiting large seeds and simply eats more of them, took over. Unlike the event of 1977, this time, larger *G. fortis* stood very little chance and the species had to make ecological adjustments to their larger and hungrier competitors. Interestingly, although speciation is a neverending process, frequent perturbations in the Galapagos environments (e.g. El Niño/La Niña events) seem to have made it faster than usual - most lineages of finches on the archipelago still interbreed (Lamichhaney et al. 2015). Additionally, population mean beak shape and size from a few decades ago when the studies started are significantly different from recent measurements in the same taxa (Grant & Grant 2003).

Jonathan Losos and his collaborators have used island systems extensively over the years to study the ecology and evolution of lizards and offer another prime example of fortuity in a recent report. Namely, Donihue et al. (2018) demonstrated for the first time that hurricanes can cause selective mortality on the basis of phenotypic traits. The team surveyed the morphology of the endemic

Anolis scriptus on the Turks and Caicos Islands (Water Cay and Pine Cay), but did not anticipate the forthcoming record-breaking storms – hurricanes Irma and Maria (with wind speeds of up to 200 and 240 km/h, respectively). Going back to the islands post storm and resurveying the same transects revealed evolution by natural selection in action, more specifically directional selection. The authors quantified significant morphological changes on both islands linked to improved clinging ability (larger toepads [Crandell et al. 2014], proportionately longer humeri [Kolbe 2015] and shorter femurs [Donihue et al. 2018]) and found a significant decrease in variance within the succeeding samples (indicating directional selection).

Cases of fast evolutionary change and the questionable species statuses of Galapagos finches beg the question of determinism in evolution. Anolis lizard communities from the Caribbean have seemingly remained unchanged since the Miocene (Sherratt et al. 2015). Interestingly, these communities of lizards occupy all the great Antilles, but habitat specialists (ecomorphs) are genetically distant between islands (Losos et al. 1998). It seems that communities remain the same between islands and geological time, but not genetic lineages (ruling out vicariance as the driver of these examples). Furthermore, replicate adaptive radiations between islands imply adaptation as the main culprit for this outcome, rather than constraint. Galapagos finches seem to follow similar adaptive tendencies constantly evolving beak size and shape, but unlike Caribbean anoles they still fail to form distinct genetic lineages keeping their species status questionable. This might be a result of either their much higher dispersive capabilities, or the sheer frequency of environmental vagaries; nonetheless neither is as relevant to this thesis as are the most prominent common denominators of the afore-mentioned examples – islands and the quantum and quality of data collection they offer. These little containers holding often simplified, or at least smaller pieces of environment clearly present researchers with the highest level of detectable fortuitous events offering much convenience for proper evolutionary-ecological data collection.

Unquestionably, experimental laboratory research is technically the safest way of drawing causal conclusions since contingencies can be heavily controlled,

but natural systems are full of contingencies. Thus, dense long-term datasets from free-ranging animals offer invaluable insight on population functioning. Repeated species-specific studies can further overcome bias from confounding factors and bring about sound conclusions with species-wide relevance. On the other hand, controlled experiments also offer indispensable insight and replicates make for more solid conclusions, but the scope can be narrow (nevertheless, this is still the best way of uncovering the genetic architecture and/or physiological processes underlying phenotypes). Laboratory and field studies on lizards from the Dalmatian coast offer a glance into the benefits and shortcomings of both approaches. Field effort demonstrated the existence of three colour morphs (orange, yellow and white) of the Dalmatian Wall lizard (*Podarcis melisellensis*) on the island of Lesnovo in Croatia, and differentiated the orange morph as longest (snout-vent length) and with a disproportionately large head (Huyghe et al. 2007). It was only later, after more in-depth laboratory measurements that the orange morph revealed a harder bite force which was linked to larger internal and external jaw adductors (Huyghe et al. 2009); even later, molecular analyses showed that the three colour morphs may represent weakly distinct gene pools, possibly indicating assortative mating (Huyghe et al. 2010) and opening even more exciting areas for future research. Close by, on a smaller Dalmatian island Herrel et al. (2008) demonstrated that, after outcompeting the native Dalmatian wall lizard and causing its local extinction, the introduced Italian Wall lizard (*Podarcis sicula*) shifted to a predominantly plant-based diet and in a matter of only 36 years (~30 generations) went through a dramatic evolutionary event of intestinal morphology. Namely, unlike their nearby, predominantly carnivorous population of origin, these lizards' necessity to tear and digest more cellulose brought about their higher bite force and the presence of cecal valves that slow down food passage, allowing for fermentation processes that break down cellulose. Cecal valves are absent from known conspecifics, but their presence in hatchlings and juveniles of this population suggests a genetic basis. Nevertheless, the authors point out the necessity of future controlled laboratory investigations on the potential roles of maternal effects and/or phenotypic plasticity in the divergence between populations.

Although, what is the appropriate sample to study phenotypic plasticity? – Gianoli & Valladares (2012) state: “advances in the understanding of the ecological significance of phenotypic plasticity in nature can be achieved if representative samples of the genotypic diversity of natural populations are included in the study”. They build this argument on top of the ongoing debate over the use of clones (or genetic families) across ecological gradients when studying plasticity. While this is the cleanest approach regarding confounding factors, it also offers less reliable results to be discussed in the context of nature. Indeed, “only a small number of original genotypes would be sampled in the field” (Gianoli & Valladares 2012). Drawing a parallel between samples collected for experiments *vs.* their native population and island populations *vs.* other conspecific populations paints the idea of islands as “natural laboratories” – “places where one can find numerous experiments in progress at any time” (Wallace 1978). If the marriage of controlled laboratory experiments and those based in nature can give the most objective insight, then islands may well be their lovechild of compromise.

The island of interest to the thesis at hand – Golem Grad has already presented its role as a natural laboratory. The local dense population of dice snakes (*Natrix tessellata*) allowed for the collection of more than 5,000 individuals in four years (Ajtić et al. 2013). These data provided biological and ecological insight: known maximal body size (at the time) was extended by ~20%, maturity was reported to be attained at a longer snout-to-vent length, and a co-occurrence of three constantly present colour morphs in both sexes was documented. Interestingly, Ajtić. et al. (2013) suggested a very fast recruitment rate due to low numbers of subadults, making Golem Grad an ecosystem more to the likes of tropical systems (for dice snakes). On another note, that is – on-another-island-dwelling-water-snake-species-from-the-New-World, the Northern Water Snake (*Nerodia sipedon insularum*), islands have further demonstrated the levels of convenience they offer to the amassment of data and insight. Specifically, unlike Golem Grad dice snakes, Water Snakes inhabiting western Lake Eire’s island region are slower growers than other conspecifics (King 1986), but similar “showers” as Golem Grad dice snakes (e.g. three insular colour morphs, King R.B. 1987).

Such studies have allowed for the detection of high variation within traits and on several levels of organization, notably inter-individual growth divergence within Water Snakes (King et al. 2016). While population mean trait values are informative, the authors demonstrated that variation among individuals is so high that some asymptotic size projections fall out of population means. Islands facilitate the long-term continuous annual recaptures and measurements of individuals, crucial for individual-based models. In light of the ever-growing awareness of the importance of individual heterogeneity to detailed and ever less biased ecological and evolutionary studies (Hamel et al. 2018), future effort should be allocated to such capture-recapture (CR) studies. These notions are of particular importance to the understanding of different facets of life history theory, particularly having in mind the huge variety of traits, their common correlative nature (e.g. body size has a ubiquitous effect on other traits [Peters 1983]) and finally the resulting broad spectrum of animal life-histories. Broad categories have been developed according to common trait covariation such as the slow-fast continuum of life-history tactics, or long- and short-lived animal life histories (Stearns 1992). Nevertheless, as helpful as broad definitions and categories are, they cannot embrace the full complexity of the processes under focus and they may mistakenly clump organisms or individuals together promoting errors; identifying (individual) heterogeneity and implementing it into the definition of finer life-history categories will be useful.

Although broad and complex to begin with, Sol and Maspons (2015) argue, convincingly so, the necessity of further integrating life-history theory in a behavioural framework with the goal of a more unified theory. Indeed, Wong and Candolin (2015) demonstrate that understanding behavioural responses can help anticipate the impact that human-induced environmental change can have on populations, communities and ecosystems. Behavioural phenomena are nevertheless often open to interpretation, and furthermore due to the vastness of some ecosystems and the timid nature of many living organisms also difficult to witness. Amassing behavioural observations in order to identify patterns is thus

usually an exceptionally ungrateful task, making islands adequate vectors for observation due to (often) easier data collection (Wallace 1978). This is to a big extent likely a consequence of island tameness due to lack of exposure and/or predation (Cooper et al. 2014; Rasheed et al. 2017), a phenomenon even Darwin himself observed (“a gun is here [Galapagos] almost superfluous”) after pulling iguana tails and sitting on giant tortoises. This notion is often contested by the theory of a founder effect initiated by bold dispersal-prone individuals that are likely the first and/or the most common colonizers (Cote et al. 2010; Brodin et al. 2013). Regardless, Golem Grad Island has already managed to provide sufficient dense behavioural observations to study even such phenomena. Golubović et al. (2013a, 2013b) demonstrated that habitat and behaviour correlate nicely, tortoises exposed to the rugged island landscape being much more prone to risk-taking behaviour and encouraged to overcome obstacles than genetically hardly distinguishable (unpublished data) mainland (Konjsko village, Macedonia) conspecifics. Interestingly, some insular birds are known to tone down their songs (Grant 1965; Fitzpatrick 1998; Roulin & Salamin 2010) and others even their plumage (Hamao & Ueda 2000; Baker et al. 2006), both likely the result of changing sexual selection pressure (Andersson M.B. 1994).

Finally, besides my primary interest in fundamental research due to sheer curiosity, its application is inevitable and brings a profound sense of satisfaction when applied to successful conservation. A system bordering Golem Grad Island’s host lake of Lake Prespa – Lake Mikri Prespa in Greece tells one such story. Until the end of the previous century the region faced constant changes in human population and local agricultural and farming practices (Catsadorakis & Malakou 1997). This affected the local environment drastically by reducing the surface area of wet meadows around the lake precluding some birds from breeding completely (e.g. Glossy Ibis), or simply lowering their numbers (e.g. Dalmatian pelican, pygmy cormorant, heron species, the ferruginous duck etc.). Activities of the Life Project “Conservation of priority bird species in Lake Mikri Prespa” (Number LIFE2002NAT/GR/8494) implemented between 2004–2007 and based on fundamental research and cooperation with the local community managed to triple the surface area of wet meadows and eventually saw the return

of breeding Glossy Ibises, and now Mikri Prespa holds the largest breeding population of Dalmatian pelicans in the world (“Annual and final Project Reports,” 2007). Unfortunately, not many examples are so encouraging – a recent reintroduction endeavour of 11 Eastern black rhinos resulted with the death of all individuals because of lack of adaptation period and salt water poisoning, all a result of failure to follow instructions based on fundamental research (“Translocated rhinos die in Tsavo East | Save the Rhino International,” 2018). Sometimes conservation measures like reintroductions seem straightforward, but systematic research can point out crucial, but often not obvious effects. For example, Bertolero et al. (2018) describe a release cost to the survival of Hermann’s tortoises introduced to an already present population. Such insight might primarily even seem obvious or unnecessary, but it can easily make the difference between life and death and prevent fates such as the ones of the Eastern black rhinos.

An ancient Hindu text, the *Bhogala Purāna* states: “The tortoise bears the burden of the whole world.” While in its literal sense this is a gross overestimation, I can confidently say that a couple of thousand tortoises from Golem Grad, Macedonia do bare a big part of the burden of this thesis. The island nature of this population has facilitated the amassment of dense individual CR datasets of tortoises of all ages, spanning the bigger part of the population. At the naive beginning of my endeavours on Golem Grad (in 2009) I wanted to learn and know everything. As more experience and extra knowledge accumulated my eyes were opened to everyday limitations due to the lack of resources, difficult logistics and sometimes simply disappointment and lack of motivation. If the last one prevails it can have dangerous consequences, but when the three are simultaneously taken into account in the presence of a very generous data-sharing system, then relevant but reasonable questions materialize.

At the very beginning of this thesis, inquiry into a tortoise’s extremely delayed maturity started to take the form of several small questions. Notably, what do the terms “juvenile” or “subadult” entail during (almost) a decade of immature life? – in this manuscript the issue will be approached via variation exploration of selected life-history traits and sexual hormones. Growth and body

size, survival, and testosterone levels will be explored on an individual- and population-mean scale, but most importantly, with age-specific considerations. As for adult sexually mature tortoises, seemingly common same-sex sexual behaviours (SSB) among males piqued researchers' curiosities initiating the exploration of proximal and ultimate causes of SSB with the help of dense behavioural datasets. Ultimately, the direction of sexual selection will be explored under the steering wheel of biased OSR in this promiscuous sexually coercive species. This story will synthesize various datasets (CR, experiments, dissections, hormones) amassed throughout the last decade of work on Golem Grad Island and try to envisage the fragile fate of this population, that may have already been sealed.

Last but not least, the potential conservation implications of such work will be discussed, placing an accent on these systems in the developing world. Non-profitable long-term fundamental research is of no interest in these areas, thus conservation has drifted from a research-based necessity to merely good-on-paper results from pro-forma short-term activities. The system ends up satisfying detached international investors and local stakeholders with deep pockets, but does very little for nature conservation, if anything at all.

2. STUDY SYSTEMS & SETTING*



* Please find detailed statistical methodologies in the appendix.

2.1 STUDY SPECIES

The Hermann's tortoise (*Testudo hermanni*) is a medium sized terrestrial chelonian (130 – 180mm average carapace length) inhabiting Europe's Mediterranean. It is comprised of two subspecies, *T. h. hermanni* to the west of Po Valley in NE Italy and *T. h. boettgeri* to the east covering a large part of the Balkan Peninsula (Bertolero et al. 2011).

Males are the smaller sex in the Hermann's tortoise (Djordjevic et al. 2011). This is only evident in mature individuals; immature tortoises cannot be sexed with certainty. Unlike closely related species (e.g. *T. graeca*), the Hermann's tortoise has a pronounced horny claw-like scale at the tip of the tail. It is more pronounced in males, and it is used to aggressively stimulate females during courtship. Hermann's tortoises practice sexual coercion; courtship entails chasing, head bobbing, biting, and mounting, during which, more often than not the female actively attempts to flee (Hailey 1990; Sacchi et al. 2013). Mounting and copulation are often accompanied with high pitched male vocalization (Galeotti et al. 2007). Maximum clutch size in females of the eastern subspecies is nine with an average of 4.3. Sex determination is temperature dependent (Pieau 1996). Among populations, operational sex ratio (OSR) can be biased in favour of either sex (Hailey 1990; Hailey & Willemsen 2000). When present, the origin of OSR bias is not yet clear.

Mediterranean *Testudo* species accumulate growth rings on their shells that correspond to their periods of active thermoregulation intersected by prolonged hibernation events (Lagarde et al. 2001; Bertolero et al. 2005). Hermann's tortoises are indeterminate growers, with growth usually decelerating at maturity. Once this happens, growth rings become narrow and eventually blend into each other adding up to a smooth carapace in old individuals (+25 years). This offers a very convenient method of age estimation for immature and recently matured individuals. On average, before maturity Hermann's tortoises grow 10mm/year (Willemsen & Hailey 2001) and can become mature at various body sizes. Size at maturity is the proximate cause of variation in adult size (Willemsen & Hailey 1999).

Hermann's tortoises occupy various habitats ranging from cultivated plains and open Mediterranean scrublands to closed forests (Longepierre et al. 2001). Adults can travel up to 80m daily (Hailey 1989; Rozyłowicz & Popescu 2013; Sibeaux et al. 2016), and in doing so can encounter various hindrances depending on habitat (Golubović et al. 2013a, b, 2014). Tortoises seem to experience habitat-specific locomotor challenges, ranging from dense shrubs slowing down progression, to steep, rocky areas promoting more frequent flipping of tortoises on their dorsum (Golubović et al. 2013b, 2014).

2.2 STUDY SITES

Two populations of eastern Hermann's tortoises were monitored for 10 and 8 years (from 2008 and 2010 until present day) on Golem Grad island (40°25'09"N, 20°59'17"E) and in Konjsko village (40°54'46"N, 20°59'17"E), respectively. Both localities are in the Prespa region of the Republic of Macedonia, situated in the far south-west of the country, bordering Albania and Greece (Fig. 1). They lay on the shores of Lake Prespa, separated from each other by a water barrier spanning ~4.5km. There are no constant human settlements in either locality; Konjsko is a popular vacation spot during the summer months when there is continuous human presence, whereas Golem Grad island does not hold accommodation and only short visits are allowed. Both localities are within the borders of National Park "Galičica", and Golem Grad additionally (on paper) enjoys the protection status of a nature reserve. The climate of the region is governed by its latitude, altitude (~850 m asl) and the buffering capacity of the lake; with both Mediterranean and continental influences it is formally defined as modified Mediterranean with mildly cold winters and hot summers (Lazarevski 1993).

Konjsko is situated on a small peninsula on Prečna Mountain (part of Galičica Mountain, Fig. 1) covering an area of ~20ha. Its circumference is thus mostly outlined by beaches and a land connection to the west. On this side there is no physical barrier that could prevent the dispersal of tortoises; the population is thus semi open. Centrally Konjsko summits at a small hill (Blut) covered by an oak forest. For the most part, the stony beaches are covered by undergrowth of

vines and shrubs. The habitats in Konjsko are physically generally uniform, lacking steep steps and obstacles.

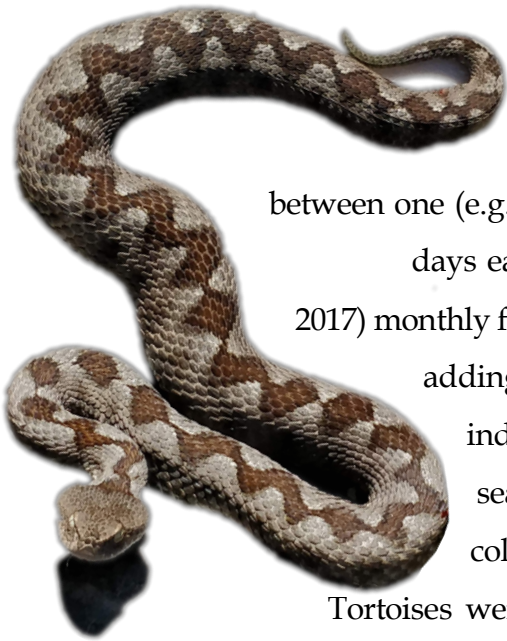
Golem Grad island covers a surface area of ~18ha; terrestrial species here are locked (no immigration or emigration). Interestingly, the island is comprised of two broadly different habitats – stony beaches mostly covered in undergrowth, and a plateau covered in a coniferous forest of the Greek juniper (*Juniperus excelsa*). They are separated from each other by 10-30m high steep cliffs; two steep accession paths exist at the southern and north-western sides of the island. Golem Grad is characterized with uneven and rocky habitats adding up to a rugged topography. Besides the Hermann's tortoise, the island is home to dense populations of three other reptile species: the wall lizard (*Podarcis muralis*), the dice snake (*Natrix tessellata*), and the horn-nosed viper (*Vipera ammodytes*, next page).

The monitored tortoise populations are genetically hardly distinguishable (unpublished data). Nevertheless, risk taking behaviours seem to reflect habitat type and configuration, Golem Grad promoting willingness to jump from high obstacles unlike Konjsko tortoises (Golubović et al. 2013a).



FIGURE 1. Lake Prespa and both study sites (outlined in yellow) in respect to the Balkan Peninsula (top right; area in red square enlarged). AL - Albania, GR - Greece, MK - Macedonia; white lines represent country borders. Image from Google Earth Pro 7.3.1.4507 (64-bit).

2.3 STUDY POPULATIONS AND SAMPLING



At both localities standardized capture-recapture (CR) studies were set up. Annually 2-18 people sampled both localities during 7-35 days assembled between one (e.g. one seven-day session in July 2015) to five (e.g. five days each month between May and September in 2016 and 2017) monthly field sessions. Overall, on Golem Grad 32 field sessions adding up to 195 search days enabled us to process 1,839 individuals, amassing 14,119 recaptures. In Konjsko 48 search days during 22 field sessions enabled the collection of 595 recaptures from 887 individuals.

Tortoises were searched for visually. Before capture, in order to limit disturbance, location and behaviour (Table 6 in the appendix) were recorded first. Subsequently individuals were sexed if mature (a subsample of immature individuals became sexually dimorphic throughout the study period), aged when possible, measured for straight carapace length (SCL) with callipers, weighed (BM), and permanently marked using a notche-code on the marginal-scutes (Right; Stubbs et al. 1984). During resightings behaviour was recorded first, then tortoises were recaptured to check identity, remeasured, and age was re-estimated blindly (i.e. without checking previous estimate). Individuals were rapidly released at the place of capture. After death the carapace takes substantial time to disintegrate and the scute marks often remain visible on the underlying bony tissue. This offers the opportunity of locating dead individuals and identifying them as recovered carapaces.



3. RESULTS

The results have been organized to resonate the separation of potential benefits of island research introduced in chapter 1 (from run-of-the-mill ecological insight enquiry to island-specific peculiarities, p. 1) and the broad questions raised at the end of the chapter. Sections 3.1, 3.2 and 3.3 quantify run-of-the-mill population-mean ecological parameters of Golem Grad Hermann's tortoises, each section eventually moving from run-of-the-mill to more detailed individual and/or age-specific considerations. Sections 3.4 and 3.5 move into the exploration of island peculiarities, exploring tortoise behaviour, from agility to sexuality via experiments and a behavioural CR framework. Finally, 3.6 adds a physiological backbone to some aspects from the previous sections.

3.1 GROWTH

Among 1,830 marked individuals on Golem Grad Island at the time of analysis, 289 were aged (of which 113 could *a posteriori* be sexed – 28 females, 85 males) providing 1,072 body size measurements (of which 605 belonged to individuals that could *a posteriori* be sexed – 139 females, 466 males). This subsample constitutes the individuals of known age group. In the unknown age group, 845 marked tortoises were recaptured once or more, providing a total of 4,024 body size measurements (2,012 annual size increments). Among them, 55 females and 790 males, respectively, provided 122 and 1,890 incremental measurements. Some of these individuals (N = 97, 8 females, 89 males) had been encountered for at least five consecutive years and could thus be used to build individual-based growth trajectories. Mean adult male SCL = 171.4 mm (median = 173.3 mm) and mean adult female SCL = 173.6 mm (median SCL = 173.0 mm). The largest individual measured was a male of 218.2 mm SCL; the largest female measured 211.1 mm SCL. Both of these individuals are part of a subsample of 121 individuals with extremely smooth shells (i.e. very old), the smallest being 155.5 mm long. The smallest individual on the island measured 32.7 mm.

TABLE 1. Breakdown of observations (Obs) and individuals (Ind) obtained from free-ranging Hermann's tortoises of known age (289 juveniles or young adults). O-F and I-F stand respectively for observations and numbers of females, idem for males (O-M and I-M). SCL means straight carapace length (mm), both sexes pooled (SCL F+M) and separately for females and males (SCL F, SCL M). Means are provided \pm their standard deviation (in brackets, σ). The proportion of tortoises that could be sexed increased with age.

Age	Obs	Ind	O-F	I-F	O-M	I-M	SCL F+M	SCL F	SCL M
1	104	95	2	1	6	6	41.3 (3.9)	41.9 (2.9)	44.3 (1.8)
2	110	97	6	6	13	12	49.8 (4.7)	48.3 (3.1)	51.6 (5.5)
3	118	86	11	9	26	20	58.0 (4.8)	57.4 (5.8)	60.8 (4.6)
4	99	75	9	6	40	29	66.1 (5.3)	64.2 (3.6)	68.2 (4.8)
5	108	79	9	5	55	39	76.2 (6.8)	78.2 (9.8)	78.1 (6.9)
6	108	82	17	13	69	21	88.8 (8.1)	90.3 (8.2)	87.9 (6.5)
7	120	101	24	17	58	50	96.9 (8.7)	99.9 (11.2)	97.6 (7.4)
8	97	81	19	16	51	40	106.7 (9.9)	110.8 (10.0)	108.3 (9.2)
9	58	52	16	15	32	28	114.5 (10.8)	121.6 (11.8)	112.3 (8.9)
10	56	50	10	9	40	35	123.3 (10.2)	123.6 (3.8)	124.3 (11.2)

Age	Obs	Ind	O-F	I-F	O-M	I-M	SCL F+M	SCL F	SCL M
11	35	31	3	3	30	27	128.0 (9.1)	127.1 (7.6)	129.2 (8.5)
12	27	23	6	6	21	17	142.0 (12.1)	140.7 (13.5)	142.3 (12.0)
13	11	10	3	3	8	7	146.1 (8.9)	154.0 (7.7)	143.1 (7.8)
14	8	8	2	2	6	6	150.6 (16.8)	170.5 (19.1)	144.0 (10.6)
15	7	6	2	2	5	4	153.6 (3.9)	158.5 (0.7)	151.7 (2.4)
16	5	4	0	0	5	4	157.6 (7.1)		157.6 (7.1)
17	1	1	0	0	1	1	167 (0)		167 (0)
Total	1,072	289	139	28	466	85			

Mean adult SCL in Konjsko was 21mm longer in females than males (192.5 vs. 171.5), the largest female (237.0mm) being 23mm longer than the largest male (214.0mm).

3.1.1. Age-specific variation in body size (VBS)

Visual exploration of the frequency distribution of individual SCLs for each of the first 9 years of life revealed two abrupt shifts in VBS separating three groups of juveniles: very young individuals measured during their first year of life (the first shift occurs between one and two years), young two- to four-year-old individuals (the second shift occurs between four and five years), and then individuals older than five years (p. 34, Fig. 7; see Table 1 for shifts in σ between age classes). This step pattern suggests that VBS increases with age in a non-regular step-wise way.

3.1.2. Population and cohort mean asymptotic sizes

The von Bertalanffy and logistic growth models fitted on the known age group yielded drastically different outcomes (p. 35, Table 9). Nevertheless, both models showed similar broad fitting (Bertalanffy $R^2 = 7.5$; Logistic $R^2 = 7.2$), but due to the overly generous estimates of the von Bertalanffy model (Hermann's tortoises cannot reach 500 mm in SCL, unless perhaps hormonal implants are used) we retained the logistic model for the sex-specific analyses. This subset contained one- to 15-year-old individuals of both sexes and proposed similar asymptotic sizes in females and males ($SCL_A \pm 1$ standard error [SE] = 178.1 ± 8.0

mm vs 172.4 ± 4.6 mm, respectively; p. 34, Fig. 8), suggesting that before maturity and during the first years after its onset, body size and growth rate do not differ considerably between the sexes.

In individuals of unknown age, the three-parameter von Bertalanffy growth equation yielded SCL_A and SCL_0 of 180.7 ± 0.9 and 34.6 mm, respectively. These values were closer to the logistic model of the known age group compared to the output of the Bertalanffy model, suggesting that the growth patterns of juveniles and adults differ. Sex-specific analyses of the individuals of unknown age indicated that females should attain a larger size than males, both considering hatchling (SCL_0) and asymptotic adult sizes: 38.7 mm versus 33.9 mm at hatching, and 188.7 ± 6.3 mm versus 179.9 ± 1.9 mm asymptotic SCL (p. 35, Table 9).

3.1.3. Individual variation in size and growth

Bootstrapping the original sample of individuals of known age and estimating asymptotic size of each bootstrap suggests that even though there is a clear population mean asymptotic size, there exist early-age, likely immature individuals (predominantly one-to-10-year-olds) with idiosyncratic trajectories. Such individuals have driven the estimated SCL_A values of 10,000 bootstraps to range from 162.8 ± 6.2 to 189.4 ± 6.4 mm.

The asymptotic sizes based on the 97 particularly well-monitored (consecutive annual recaptures ≥ 5) individuals ranged between 152.5 ± 6.3 and 212.4 ± 9.0 mm in males, and between 180.5 ± 4.0 and 223.8 ± 12.3 mm in females. Although females exhibit the largest estimated asymptotic size, they were actually not consistently larger than males. In both sexes, asymptotic size varied greatly; the magnitude of variation was 59.9 mm in males, and 43.3 mm in females. On average, the estimated asymptotic size ± 1 SE of any given adult differed from 49% of other individually analysed adults ($SCL_A \pm 1SE$). Although our population-wide analyses predicted that tortoises from Golem Grad Island should converge to a single asymptotic size (p. 34, Fig. 8), 60.6% of individual asymptotic sizes \pm their respective 1SE fell out of the 1SE interval around the

mean SCL_A estimated from individuals of known age; this proportion was 61.7% considering individuals of unknown age (Fig. 2)

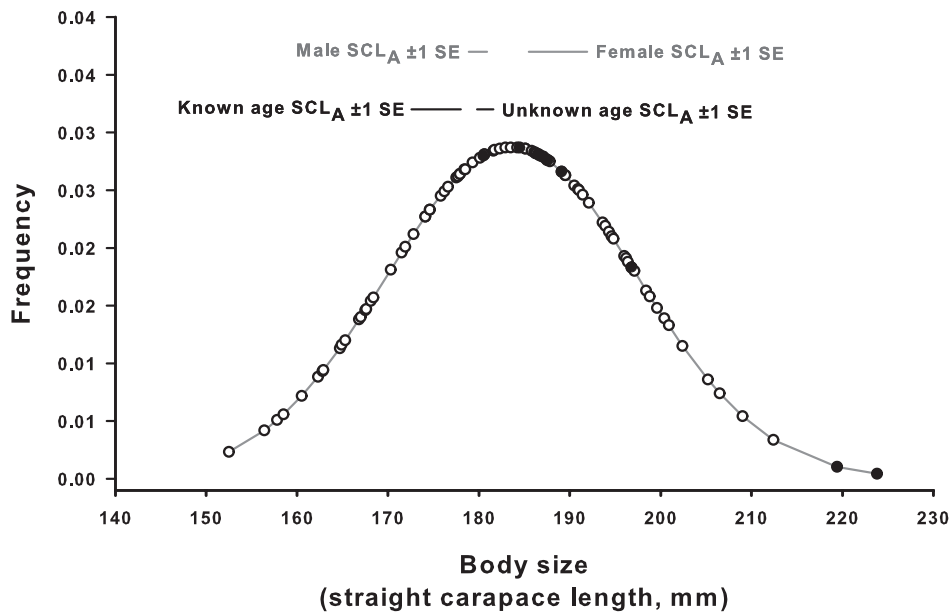


FIGURE 2. Distribution of estimated individual asymptotic sizes of Hermann's tortoises from Golem Grad Island against estimated population and sex-specific mean asymptotic sizes from Table 2. Females are marked with filled circles and males with open circles. To facilitate comparison, ranges of population and cohort mean asymptotic sizes ($\pm SE$) are displayed with four horizontal lines above the bell curve. These lines encompass a limited range of variation, accentuating the wide potential for individual asymptotic sizes

Finally, the individual-based growth trajectories showed that regardless of SCL at first capture, mature tortoises can still end up at different asymptotic size (p. 35, Fig. 9). The range of projected growth from capture to asymptotic size spanned between 0.0 and 40.3 mm.

3.2 BODY CONDITION

After model selection, variation in body condition index (BCI) was best explained by the interactive effect of sex and locality (Table 2). The variance explained by the random factor was 0.60, rendering it necessary to avoid pseudo-replication from measurements of recaptures. Konjsko tortoises exhibited higher BCIs in general ($t = 30.57, p < 0.001$), the males being worse off than the females ($t = -21.69, p < 0.001$). Boxplots of the predictions based on the best-fitted model clearly

differentiate females from Konjsko as the most fit cohort regarding BCI (p. 36, Fig. 10).

TABLE 2. Model selection procedure showing all competitive models describing the variation in body condition indices (BCIs) among Hermann's tortoises from Golem Grad island and Konjsko in order of conception. r = model rank, AIC = Akaike information criteria, w = model weight, loc = locality. Shaded row denotes selected best model.

r	Model definition	AIC	w
3	sex	18,028.80	0.3
4	loc	18,438.41	0.5
2	sex+loc	17,485.90	0.2
1	sex*loc	17,042.82	0.0

3.2.1 Fecundity and mating costs



FIGURE 3. Dissection of a fecund female from Konjsko (Female K in Table 3)

Dissections indicate greater fecundity of Konjsko females (Fig. 2 & Table 3; island females having no eggs in oviducts), additionally, Golem Grad dissected female reproductive systems almost completely lacked follicles (Table 3).

TABLE 3. Fecundity and body reserves data obtained from freshly dead and dissected female Hermann's tortoises from Golem Grad Island (GG) and Konjsko village (K). These individuals' BCIs in respect to their respective cohort mean BCIs can be found in Fig. 10 (p. 36).

	Female K	Female GG 1	Female GG 2	Female GG 3
Total mass	2348g	651g	914g	771g
No. of eggs	7	0	0	0
No. of follicles (0.5-1 cm)	35-40	0	0	0
No. of follicles (1-2 cm)	5	2	8	0
No. of follicles (>2 cm)	8	2	0	0
Egg + follicle proportion	10.01%	0.97%	2.14%	0.14%
Fat body proportion	0.30%	0.50%	0.00%	0.00%

3.3 SURVIVAL, POPULATION SIZE & SEX RATIO

3.3.1 Adult survival

3.3.1.1. Golem Grad

After model selection (Table 4) the best-fitted model implied different capture probabilities between years, sexes and heterogeneity classes. On average high capture heterogeneity females had lower annual capture probability (0.56, CI 0.48-0.63) than their male counterparts (0.63, CI 0.60-0.66). The same trend was evident among low capture heterogeneity individuals (females = 0.06[0.02-0.18], males = 0.41[0.32-0.50]). Recovering a male carapace from a dead individual (0.61[0.39-0.79]) was more likely than recovering one from a female (0.39[0.32-0.46]). Survival was strongly sex dependent, adult females expressing surprisingly low survival probabilities of 0.84 (CI 0.80-0.87). Adult males, on the other hand express much higher mean annual survival of 0.97 (CI 0.96-0.98).

TABLE 4. Model selection procedure showing all competitive models regarding adult Hermann's tortoise survival on Golem Grad island in order of conception. r = model rank, k = number of parameters, Dev. = deviance, QAIC = Akaike information criteria, w = model weight, loc = locality, het = heterogeneity. Shaded row denotes selected best model.

r	Model definition		k	Dev.	QAIC	w
	Survival	Recapture				
6	cst	cst	2	12531.39	12535.39	0.3
4	cst	het	5	12464.34	12474.34	0.2
5	cst	sex	3	12520.16	12526.16	0.3
3	cst	sex*het	8	12433.36	12449.36	0.2
2	cst	sex*het*year	50	10185.95	10285.95	0.0
1	sex	sex*het*year	51	10143.33	10245.33	0.0

3.3.1.2. Konjsko

After model selection (Table 5) adult Konjsko tortoises expressed constant capture probabilities across sexes, without capture heterogeneity. Probabilities to capture adult tortoises varied between years, likely due to field effort. Years of very low field effort (2012-2015) yielded capture probabilities ranging between 0.03-0.05, whereas years of high field effort (2010, 2016 & 2017) resulted with higher probabilities of 0.36-0.44. The best-fitted model implied sex-

specific survival. Nevertheless, ΔAIC between this model and the one suggesting constant survival among sexes was only 2.5 (Table 5) and according to the former there was no significant difference in adult survival estimates. Consequently, further discussion will be based on the model with less parameters (Table 5, highlighted row) demonstrating that annual adult survival among Konjsko tortoises is 0.93 (95% CI 0.90-0.95).

TABLE 5. Model selection procedure showing all competitive models regarding adult Hermann's tortoise survival in Konjsko in order of conception. r = model rank, k = number of parameters, Dev. = deviance, QAIC = Akaike information criteria, w = model weight. Shaded row denotes selected best model.

r	Model definition		k	Dev.	QAIC	w
	Survival	Recapture				
3	cst	cst	2	2259.6	2263.6	0.3
4	cst	het	5	2253.6	2263.6	0.3
5	cst	sex	3	2259.4	2265.4	0.3
2	cst	year	8	1833.1	1949.1	0.0
1	sex	year	9	1928.6	1946.6	0.0

3.3.2 Early-life age-specific survival

The goodness-of-fit tests were significant ($\chi^2=127.35$ and 72.09 , $df=60$ and 31 , respectively, $p<0.001$) with significant transience and trap-dependence (both $p<0.001$), suggesting strong survival or recapture heterogeneity.

After model selection, regarding recapture probability two to six-year olds formed a separate cohort whereas all further age classes up to ten-year olds were considered separately. All are site dependent, while only those from the Plateau experience recapture heterogeneity (lowering AIC by 71). Among them, the class with higher recapture probabilities ranged between 0.56 and 0.71, the low recapture class from 0.01 to 0.07 and Beach tortoises somewhere in the middle between 0.32 and 0.40. All recapture probabilities express additive time variation. Exploring different parameterizations of the age-effect on survival resulted with a logarithmic to linear relationship reaching a plateau at five to seven years of age, or a discrete model summing at the age of five (ΔAIC between these models ranged between 0.6 and 1.3, Table 6; models whose ΔAIC 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 during the first year to 0.86 when six 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 (p. 36, Fig. 11). Superimposing the discrete model estimates (despite being slightly lower due to lack of separation of Plateau females) showed a broad overlap of confidence intervals (p. 36, Fig. 11).

TABLE 6. Model selection procedure showing all competing models for 1-10-year-old Hermann's tortoises from Golem Grad 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, _ = survival plateau.

r	Model definition		k	Dev.	AIC	w
	Survival	Recapture				
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	[age1;2-10]+year	32	4510,6	4574,6	0,0
55	Age	[age1;2;3-10]+year	34	4473,1	4541,1	0,0
54	Age	[age1;2-3;4-10]+year	34	4412,3	4480,3	0,0
51	Age	[age1;2-4;5-10]+year	34	4345,2	4413,2	0,0
50	Age	[age1;2-5;6-10]+year	34	4290,1	4358,1	0,0
48	Age	[age1;2-6;7-10]+year	34	4227,1	4295,1	0,0
41	Age	[age1;2-7;8-10]+year	34	4160,3	4228,3	0,0
40	Age	[age1;2-8;9-10]+year	34	4156,8	4224,8	0,0
42	Age	[age1;2-9;10]+year	34	4193,6	4261,6	0,0
36	Age	[age1;2-4;5;6;7;8;9;10]+year	46	4019,2	4111,2	0,0
46	Age	[age1;2-3;4-6;7-10]+year	36	4223,0	4295,0	0,0
52	Age	[age1;2;3;4;5-10]+year	38	4341,2	4417,2	0,0

<i>r</i>	Model definition		<i>k</i>	Dev.	AIC	<i>w</i>
	Survival	Recapture				
45	Age	[age1;2;3-4;5-6;7-10]+year	38	4213,0	4289,0	0,0
47	Age	[age1;2-3;4-6;7-10]+year	36	4223,0	4295,0	0,0
49	Age	[age1;2-6;7-10]+year	34	4227,1	4295,1	0,0
56	Age	[age1;2;3;4-10]+year	34	4473,1	4541,1	0,0
38	Age	[age1;2-6;7;8;9;10]+year	40	4033,5	4113,5	0,0
44	Age	[age1;2-4;5-6;7-10]+year	36	4216,7	4288,7	0,0
39	Age	[age1;(2-6;7;8;9;10)*sex]+year	45	4029,7	4119,7	0,0
29	Age	[age1;(2-6;7;8;9;10)*site]+year	45	3947,7	4037,7	0,0
31	Age	[age1;(2-6;7;8;9;10)*H]+year	50	3942,5	4042,5	0,0
30	Age	[age1;(2-6;7;8;9;10)*site*H]+year	60	3920,1	4040,1	0,0
25	Age	[age1;(2-6;7;8;9;10)*site(P*H)]+year	53	3926,6	4032,6	0,0
33	Age	[age1;(2-6;7;8;9;10)*sex*site*H]+year	80	3899,4	4059,4	0,0
35	Age	[age1;2-6;(7;8;9;10)*site(P*H)]+year	51	3997,0	4099,0	0,0
28	Lin	[age1;(2-6;7;8;9;10)*site(P*H)]+year	47	3943,6	4037,6	0,0
34	Quad	[age1;(2-6;7;8;9;10)*site(P*H)]+year	47	3973,9	4067,9	0,0
21	Log	[age1;(2-6;7;8;9;10)*site(P*H)]+year	47	3936,9	4030,9	0,0
24	Age_9	[age1;(2-6;7;8;9;10)*site(P*H)]+year	52	3928,3	4032,3	0,0
26	Lin_9	[age1;(2-6;7;8;9;10)*site(P*H)]+year	46	3940,8	4032,8	0,0
16	Log_9	[age1;(2-6;7;8;9;10)*site(P*H)]+year	46	3935,9	4027,9	0,0
19	Age_8	[age1;(2-6;7;8;9;10)*site(P*H)]+year	51	3928,5	4030,5	0,0
20	Lin_8	[age1;(2-6;7;8;9;10)*site(P*H)]+year	46	3938,5	4030,5	0,0
13	Log_8	[age1;(2-6;7;8;9;10)*site(P*H)]+year	46	3935,0	4027,0	0,0
18	Age_7	[age1;(2-6;7;8;9;10)*site(P*H)]+year	50	3930,1	4030,1	0,0
22	Lin_7	[age1;(2-6;7;8;9;10)*site(P*H)]+year	46	3939,1	4031,1	0,0
10	Log_7	[age1;(2-6;7;8;9;10)*site(P*H)]+year	46	3934,7	4026,7	0,0
17	Age_6	[age1;(2-6;7;8;9;10)*site(P*H)]+year	49	3930,3	4028,3	0,0
12	Lin_6	[age1;(2-6;7;8;9;10)*site(P*H)]+year	46	3934,9	4026,9	0,0
7	Log_6	[age1;(2-6;7;8;9;10)*site(P*H)]+year	46	3933,6	4025,6	0,0
9	Age_5	[age1;(2-6;7;8;9;10)*site(P*H)]+year	48	3930,3	4026,3	0,0
23	Lin_5	[age1;(2-6;7;8;9;10)*site(P*H)]+year	46	3939,5	4031,5	0,0
8	Log_5	[age1;(2-6;7;8;9;10)*site(P*H)]+year	46	3934,2	4026,2	0,0
14	Age_4	[age1;(2-6;7;8;9;10)*site(P*H)]+year	47	3933,2	4027,2	0,0
32	Lin_4	[age1;(2-6;7;8;9;10)*site(P*H)]+year	46	3961,0	4053,0	0,0

<i>r</i>	Model definition		<i>k</i>	Dev.	AIC	<i>w</i>
	Survival	Recapture				
27	Log_4	[age1;(2-6;7;8;9;10)*site(P*H)]+year	46	3941,9	4033,9	0,0
2	Age_5*site	[age1;(2-6;7;8;9;10)*site(P*H)]+year	52	3912,9	4016,9	0,2
5	Log_6*site	[age1;(2-6;7;8;9;10)*site(P*H)]+year	47	3925,2	4019,2	0,1
15	Age_5*sex	[age1;(2-6;7;8;9;10)*site(P*H)]+year	52	3923,6	4027,6	0,0
6	Log_6*sex	[age1;(2-6;7;8;9;10)*site(P*H)]+year	47	3925,2	4022,9	0,0
11	Age_5*sex*site	[age1;(2-6;7;8;9;10)*site(P*H)]+year	60	3906,8	4026,8	0,0
4	Log_6*sex*site	[age1;(2-6;7;8;9;10)*site(P*H)]+year	49	3920,8	4018,8	0,1
3	Age_5*site(P*sex)	[age1;(2-6;7;8;9;10)*site(P*H)]+year	52	3914,0	4018,0	0,1
1	Log_6*site(P*sex)	[age1;(2-6;7;8;9;10)*site(P*H)]+year	47	3921,2	4015,2	0,5

3.3.3 Population sizes & age-specific sex ratios

According to estimates, Konjsko holds a larger population of adult Hermann's tortoises than Golem Grad by 1,230 individuals. Nonetheless, males were more numerous on Golem Grad (1,737.60 [SD=15.94] *vs.* 1,211.76 [SD=89.51]), unlike the females that in comparison are barely present on the island (159.45 [SD=7.8] *vs.* 1,915.58 [123.09]). This naturally is reflected on

TABLE 7. Estimated age-specific sex ratios of Hermann's tortoises from Golem Grad island before maturity. 95% CIs are given in parentheses.

age	Sex Ratio
2-6	1.35 (1.01-1.86)
7	0.65 (0.46-0.99)
8	0.94 (0.65-1.47)
9	1.26 (0.80-2.20)
10	1.21 (0.82-1.89)
Average	1.11 (0.90-1.42)

local sex ratios, Golem Grad exhibiting an extremely male biased OSR of 10.90 (SD=0.54), as opposed to Konjsko's somewhat female-biased OSR of 0.63 (SD=0.06).

Interestingly, age-specific sex-ratio estimates during tortoises' first 10 years on Golem Grad island strongly diverge from the island's adult sex-ratio, ranging between 0.65 and 1.35 among age classes (Table 7). Mean sex ratio of the two to ten-year-old cohort of Hermann's tortoises on Golem Grad island is 1.11 (CI 0.90-1.42).

3.3.4. Survival temporal variance & canalization

The temporal variance of adult survival on Golem Grad island is clearly sex-specific, females experiencing significantly higher variation (mean=0.09) than males (mean=0.01, Fig. 4). Several bootstraps provided negative estimates of temporal variance for males. Gould & Nichols (1998) state that this is not uncommon in statistical literature and is most likely a result of very low temporal variance (zero or close); these instances were therefore regarded as zero values.

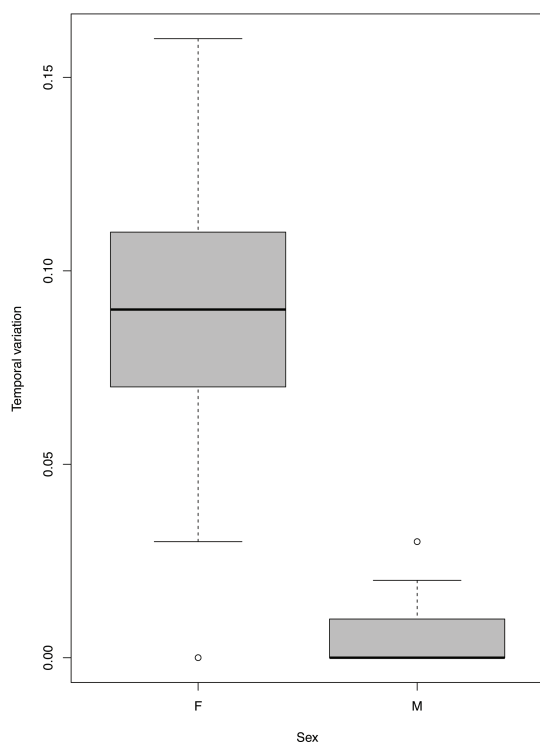


FIGURE 4. Sexual differences in the temporal variance of annual survival of adult Hermann's tortoises (SCL>130mm) from Golem Grad Island.

3.3.5. Population projections

Annual population growth rates (λ) differed between scenarios, from highest without sex-specific survival (1.04), lower with sex-specificity (0.98), and lowest when Island Plateau-female-specific survival estimates were accounted for after the age of eight (0.97). With an initial population size of 2,000 individuals (an approximation of the current population size) and an even OSR at birth, OSR stayed even in the first case scenario and the population experienced constant growth, whereas for the latter two OSR reached present day values after ~40 and ~65 years (p. 37, Fig. 12), respectively, and after 100 years they both faced a five- to nine-fold population drop (390 and 230 individuals, respectively).

3.4 SEXUAL BEHAVIOUR

3.4.1 Behavioural data in a CR framework

Between 2008 and 2014, 7,503 behavioural observations were collected on Golem Grad (Table 1 in the appendix [1A]). Adult females were more frequently inactive (i.e., partly sheltered and motionless) compared with adult males ($\chi^2 = 30.6$, $P < 0.001$, Table 1A). Many classical heterosexual behaviours (HSB) and male-to-male combats were observed, but most of the sexual behaviours recorded on this small island were same sex sexual behaviours (SSB) (Table 1A): For instance, on 295 occasions, a male was observed mounting another male (with vocalizations and/or ejaculation). SSB (i.e., mounting + courting and so on, Table 1) largely dominated among Plateau-males (74% SSB, $N = 786$), whereas HSB were more frequent among Shoreline-males (33% SSB, $N = 102$). SSB was exhibited by different individuals ($N = 363$) and thus was attributable to males at large (not only few individuals).

TABLE 8. Multistate mark-recapture (MSMR) analyses of male tortoise behaviours. Modelling probabilities of survival (S), re-sighting (p) and of transition between behavioural states (ψ) of Hermann's tortoises on Golem Grad, 2008–2014. Abbreviations: np, number of parameters; AIC, Akaike Information Criterion; sex, sex dependence; site, site dependence; state, state dependence; t, time dependence; “*”, interaction; “.” constant parameter. The selected model is indicated in bold. The initial model (model 1) fitted to the data ($\chi^2_{105} = 110.2$, $P=0.345$).

Model		np	Deviance	QAIC	$\Delta QAIC$
Modelling re-sighting probability					
$S_{(sex*site)} \psi_{(sex*site*state)} p_{(sex*site*state*t)}$	1	90	10220.4	10400.4	43.2
$S_{(sex*site)} \psi_{(sex*site*state)} p_{(sex*site*state)}$	2	34	11092.4	11160.4	803.2
$S_{(sex*site)} \psi_{(sex*site*state)} p_{(sex*state*t)}$	3	58	10257.3	10373.3	16.1
$S_{(sex*site)} \psi_{(sex*site*state)} p_{(state*t)}$	4	40	10277.2	10357.2	0
$S_{(sex*site)} \psi_{(sex*site*state)} p_{(t)}$	5	28	10391.5	10447.5	90.3
Modelling survival probability					
$S_{(sex)} \psi_{(sex*site*state)} p_{(state*t)}$	6	38	10218.3	10357.3	0.1
$S_{(.)} \psi_{(sex*site*state)} p_{(state*t)}$	7	37	10305.2	10379.2	22
Modelling transition probability					
$S_{(sex*site)} \psi_{(sex*state)} p_{(state*t)}$	8	34	10290.1	10358.1	0.9
$S_{(sex*site)} \psi_{(site*state)} p_{(state*t)}$	9	37	10284.9	10358.9	1.7

CR modelling results suggest that resighting probability was lowest for sexually active (SA) individuals involved in HSB, highest for sexually inactive individuals, and intermediate for individuals displaying SSB (Figure 5a). Transition probabilities between SSB versus HSB were sex and site dependent (Table 8, model 4). However, Δ QAIC between models 4, 6, and 8 were low. We selected model 4 (lowest absolute QAIC) for biological reasons (Burnham and Anderson 2002). Indeed, this model takes into account differential survival between sites, and this conforms, for example, to the fact that females face greater environmental difficulties on the plateau compared with the shoreline (e.g., water unavailability during summer). Furthermore, by selecting the second-best model (6), the transition probabilities between sexual behaviours were still site and sex dependent.

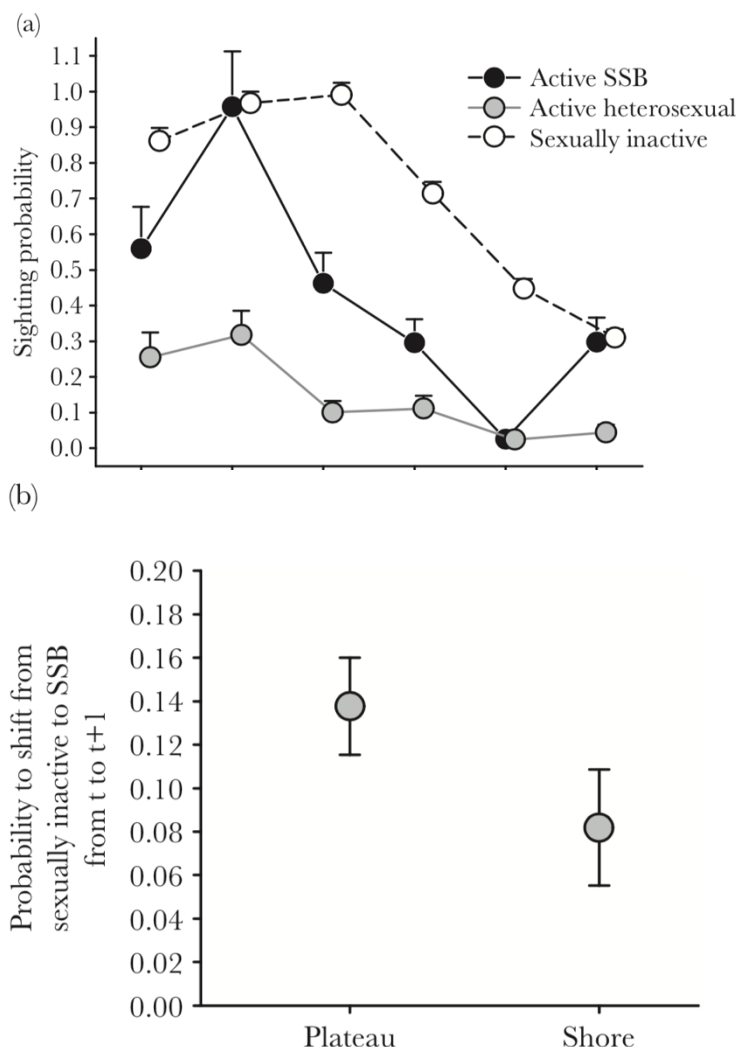


FIGURE 5. Annual re-sighting probabilities (mean \pm SE) of adult male tortoises as a function of their behaviours. A) Active heterosexual refers to males courting females or involved in male-to-male combats; Active SSB refers to males courting other males (e.g. mounting); Sexually inactive includes individuals observed: a) inactive (e.g. resting), b) active but not involved in sexual activity (e.g. feeding), and c) sexually passive (e.g. mounted) (see methods). B) Annual probabilities for a male in year t (sexually inactive) to engage in SSB in year $t+1$ in each of the two subpopulations of Golem Grad (mean \pm SE).

Individual males were not strictly homosexual or heterosexual, shifting between SSB and HSB. However, the annual probabilities for a sexually inactive male in year t to engage in SSB in year $t + 1$ were significantly higher on the plateau than on the shoreline (Figure 5b).

The annual numbers of heterosexually active individuals versus individuals exhibiting SSB were estimated using raw numbers of individuals captured each year along with their capture probabilities from the best-supported model (Table 8). Parametric bootstrapping was used to estimate confidence intervals. Each year on average, 97 ± 27 adult tortoises display HSB versus 139 ± 34 exhibiting SSB.

3.4.2. Sexual coercion (index of cloacal damage)

Mean body size differed significantly between populations, with females in Konjsko being larger (ANOVA with Box-Cox-transformed SCL as the dependent variable, $F_{1, 206} = 154.41$, $p < 0.001$). Mean body size differed significantly among the five injury-level categories without interaction between populations; larger females experienced more severe injuries (Table 9). As for swollenness, body size did not differ among the seven categories ($F_{6, 194} = 0.704$, $p = 0.646$), but the two populations were significantly different ($F_{1, 194} = 47.38$, $p = 0.001$).

TABLE 9. Statistics from the ANOVA to compare the mean body size (SCL, Box-Cox transformed data) between populations (P: Konjsko vs. Golem Grad) and among three injury levels; in total, $N = 208$ individual females were used

Source	S Sq	Df	M Sq	F	P
Intercept	7.394E+13	1	7.394E+13	1276.120	<0.001
Population (P)	4.628E+12	1	4.628E+12	79.884	<0.001
Injury level (IL)	1.208E+12	4	3.019E+11	5.211	<0.001
Interaction (IL*P)	1.632E+11	4	4.081E+10	0.704	0.590
Error	1.147E+13	198	5.794E+10		

In both populations, many large females (SCL > 170 mm) exhibited severe cloacal injuries (p. 67, Figure 16). But on Golem Grad exclusively, smaller adult females (i.e. 150-170 mm SCL) were also severely injured. This was not the case

for smaller adult Konjsko females that were spared from cloacal damage. Remarkably, many small sub-adult females ($130\text{mm} < \text{SCL} < 150\text{mm}$) along with several smaller clearly immature females ($\text{SCL} < 130\text{ mm}$; below the lower body size threshold for maturity) showed clear cloacal injuries on Golem Grad. Overall, the two populations exhibited strong divergences in the relationship between body size (hence maturity) and the prevalence of cloacal injuries.

3.5 LOCOMOTOR PERFORMANCE, HABITAT TYPE & SEXUAL COERCION

3.5.1. *Steep cliffs, carapaces & swift escapes*

In total, on Golem Grad we recovered 249 dead adults, 39 females and 210 males. The proportion of dead females with obvious carapace cracks (i.e. fallen from the cliffs) were recovered more frequently than males (8 vs. 13; $\chi^2 = 6.98$, $p = 0.008$).

3.5.2. *Locomotor performance under sexual coercion*

In the experimental enclosure when five males were placed with one female, without exception, the males immediately started chasing and harassing the female, sometimes pushing her off the edge of the opening. When alone in the enclosure Golem Grad females made the decision to exit significantly more often than Konjsko females ($\chi^2 = 1.55$, $p = 0.039$). On the other hand, when with five coercive males these differences disappeared ($\chi^2 = 0.18$, $p = 0.671$). Interestingly, Konjsko females never jumped but were rather always pushed out by coercive males (Table S4). Regardless of scenario, Golem Grad females always approached the edge of the enclosure more often than those from Konjsko (alone: $\chi^2 = 8.93$, $p = 0.003$; with five males: $\chi^2 = 41.33$, $p < 0.001$).

3.6 PHYSIOLOGICAL FRAMEWORK

3.6.1. *Sexual behaviours*

Testosterone levels (T) were compared using generalized linear models (GLM) with sex and population (male/female and Golem Grad/Konjsko, respectively) as explanatory variables and T level as the response variable. Mean T levels differed between sexes (Wald test = 215.82, $P < 0.001$) and between mainland and island populations (Wald test = 24.81, $P < 0.001$). Females

displayed markedly lower T levels compared with males; the difference between the localities appeared weak (Fig. 6). However, removing the sex effect from the model decreased AIC ($\Delta\text{AIC} = 21$), suggesting a significant population effect caused by the males: T levels were slightly albeit significantly lower on Golem Grad (4.6 ± 3.5 [SD] ng/ml), compared with Konjsko males (6.9 ± 3.3 ng/ml; Tukey post hoc test $P < 0.01$); no difference was observed in females ($P = 0.916$).

Subsequent effort focused only on males, since SA behaviours (e.g., courting, mounting, fighting), and high T levels were exclusively expressed by them. Five types of behaviours were distinguished: males found alone, mounted by another male, mounting another male, mounting a female, or during male-to-male combats (Fig. 6). A GLM revealed a significant effect of behaviour types on T levels (Wald test = 38.41, $P < 0.001$) and a significant difference between mainland and island populations (Wald test = 16.87, $P < 0.001$; as above AIC was lower in the full model, $\Delta\text{AIC} = 13.7$). Further analyses (comparing all parameters estimated or using post hoc tests) suggested that sexually passive (SP) males (found alone or mounted) exhibited lower T levels compared with males involved in the most vigorous sexual behaviours (combat) whereas other active males (mounting) displayed intermediate T levels (Fig. 6). Because SSB was observed exclusively in Golem Grad males, we restricted some analyses to these individuals: Results were unchanged (GLM analysis revealed a strong effect of behaviour type, Wald test = 37.37, $P < 0.001$). Thus, we observed a trend of higher T levels in those males sampled during most demanding sexual behaviours, without an influence of SSB. Furthermore, the significant effect of mainland/island populations and examination of Figure 6 suggest that this trend was specific to Golem Grad.

Sample sizes were small in males from the continent and in fighting island males, shedding uncertainty on some of the results above. Therefore, to examine the main effect (i.e., higher T level in the most active males) with sufficient statistical power, we used broad behavioural categories: SA ($N = 46$) versus sexually inactive males ($N = 157$). Mean T levels differed between these groups (GLM, Wald test = 19.86, $P < 0.001$) with a mainland/island effect (GLM, Wald

test = 20.77, $P < 0.001$). Overall, our results suggest a relationship between T level and sexual activity in males without specific effect of SSB.

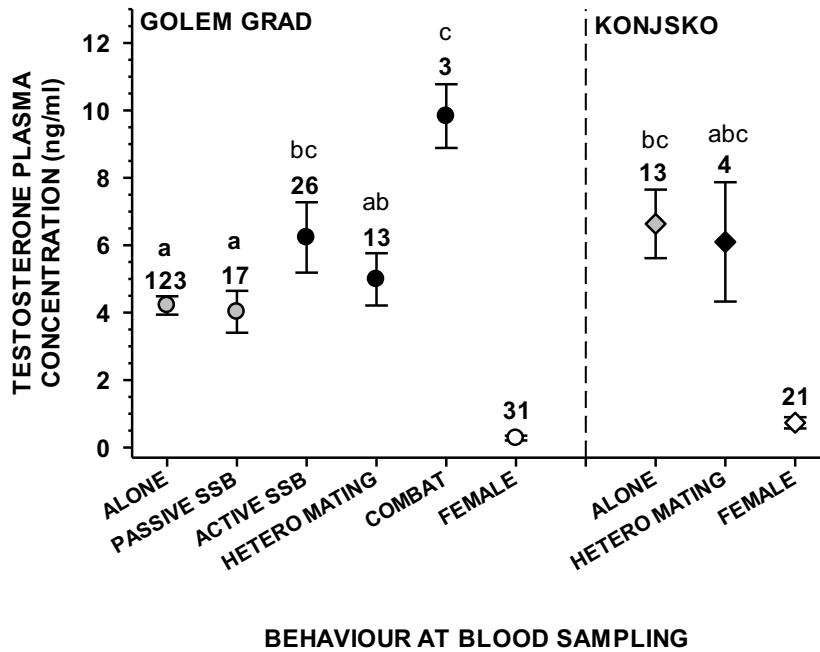


FIGURE 6. Mean plasma levels of testosterone (\pm SE) and sexual behaviours in randomly sampled free-ranging adult tortoises from Golem Grad island (circles, left panel) and from Konjsko (diamonds, right panel). Numbers above symbols stand for sample sizes. Males found alone (ALONE) or mounted by another male (PASSIVE SSB) were considered as sexually passive (grey circles and grey diamond). Males mounting another male (ACTIVE SSB), mounting a female (HETERO MATING) or during male-to-male combat (COMBAT) were considered as sexually active (black circles and black diamond). Females (open circle and diamond) were not observed sexually active. Note that SSB were observed only on Golem Grad. Strong sex differences and population effects were observed (see text for details). Letters denote significance differences among groups of males.

3.6.2. Male maturity

The onset of reproductive maturity should follow a spike in T levels due to the activation of endocrinological pathways (Nelson 2005). The dashed line in Figure 13 (p. 37) indicates that males reach maturity on Golem Grad at a minimal size of 115mm SCL. Females never show an increase in T levels. T levels thus seem to be a good indicator of maturity in males and can be used as a tool to sex sex-ambiguous males that have already reached maturity given they exhibit high T levels at the time of sampling.

4. SELECT FIGURES & TABLES

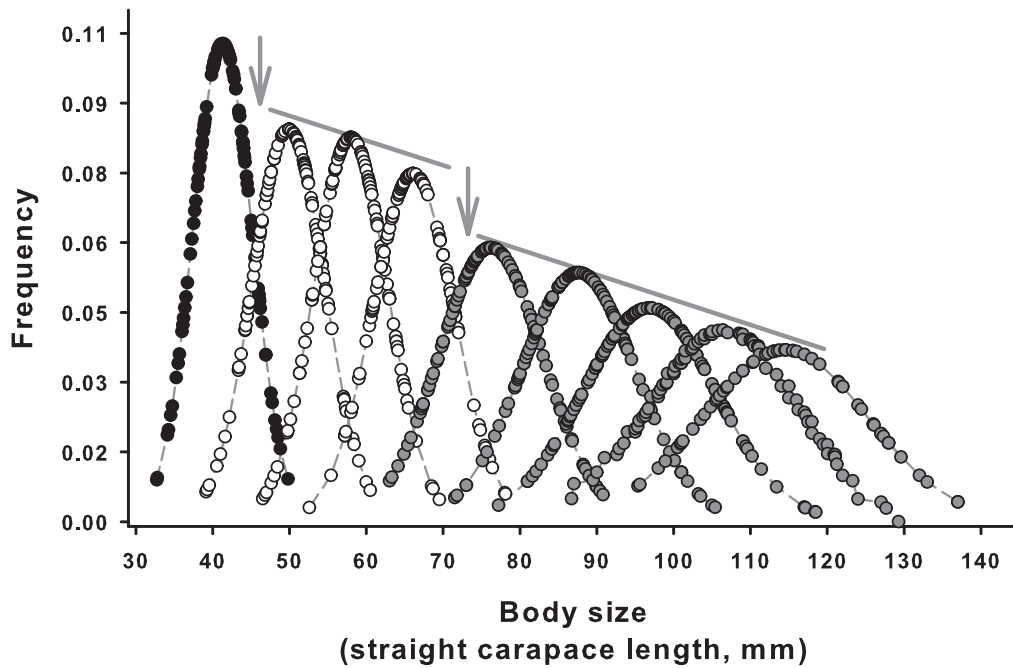


FIGURE 7. Distributions of body sizes (straight carapace length, mm) within each of the first 9 years of Hermann's tortoise (*Testudo hermanni*) life from Golem Grad Island. Each curve stands for one age class from 1- to 9-year-old individuals (from left to right). Each circle represents the measurement collected in individuals of known age (several individuals were recaptured over years and are represented in more than one cohort, see text for details). Two distribution shifts (arrows) separate three main age cohorts. They are, respectively, indicated in black (1-year-old individuals), white (2- to 4-year-old individuals), and grey (5- to 9-year-old individuals)

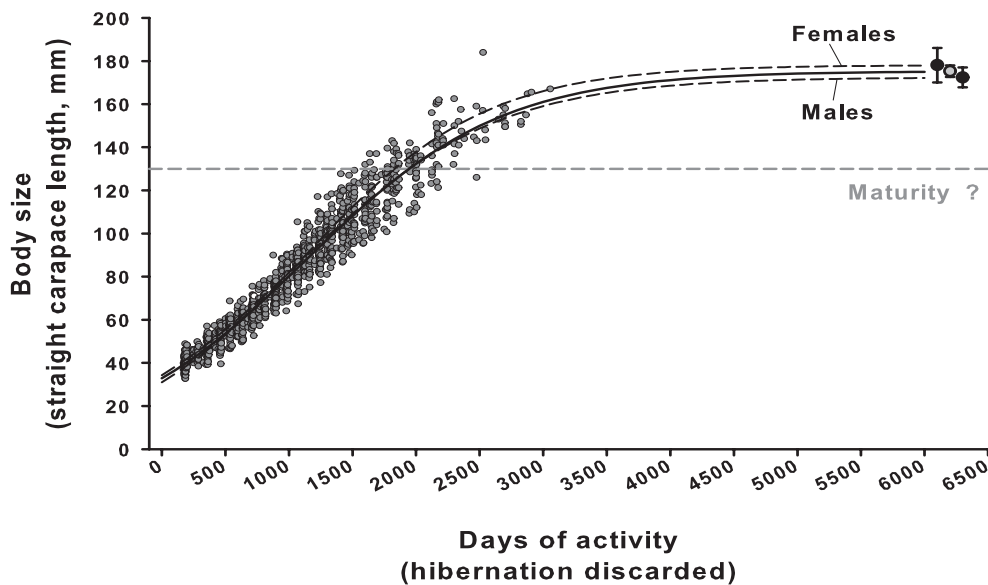


FIGURE 8. Estimated mean (solid line) and sex-specific (dashed lines) growth trajectories and mean asymptotic sizes (± 1 SE, indicated with light grey circles) superimposed against raw individual sizes (dark grey circles) of Hermann's tortoises of known age. The horizontal grey dashed line denotes size at maturity obtained from the literature (Bertolero et al. 2011)

TABLE 10. Population and cohort (sex) mean estimates of growth parameters obtained via growth models (Bertalanffy and logistic) built on the known age and unknown age datasets of Hermann's tortoises from Golem Grad island. Sample size is indicated (n). F, M, k, SCL_A , SCL_0 and R^2 denote female, male, growth rate, asymptotic SCL (mean \pm SE), SCL at birth and coefficient of determination, respectively. Analytically obtained SCL_0 values are denoted with an asterisk (*).

Source	n	k	SCL_A	SCL_0	R^2
Unknown age	2,034	0.0003	180.7 \pm 0.9	34.6*	2.23
Unknown age F	123	0.0005	188.7 \pm 3.2	38.7*	2.36
Unknown age M	1,911	0.0003	179.9 \pm 1.0	33.9*	2.20
Known age, logistic	1,072	0.001	175.3 \pm 2.7	32.8	7.24
Known age, logistic F	107	0.001	178.1 \pm 8.0	29.2	8.92
Known age, logistic M	423	0.001	172.4 \pm 4.6	34.0	7.61
Known age, Bertalanffy	1,072	0.0001	511.8 \pm 75.5	25.9	7.45

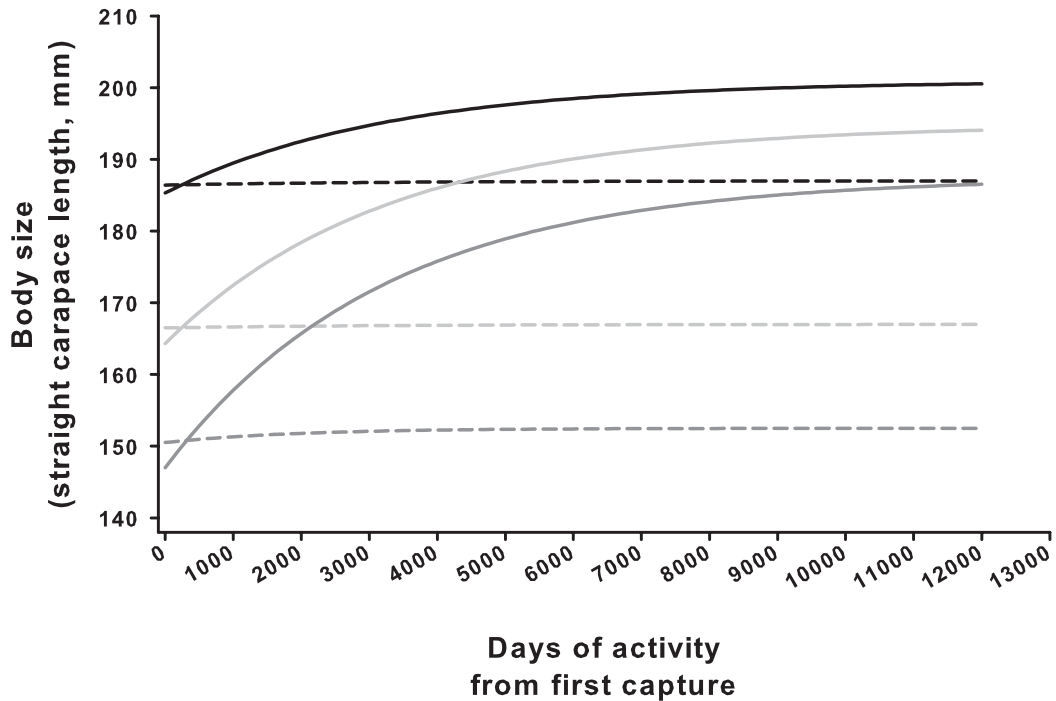


FIGURE 9. Estimated individual growth trajectories of three pairs of adult Hermann's tortoises of unknown age from Golem Grad Island with similar straight carapace lengths at the time of first capture, monitored during at least five consecutive years. Each pair is indicated with a colour pattern (black, light and dark grey) and with two line types (solid vs. dashed)

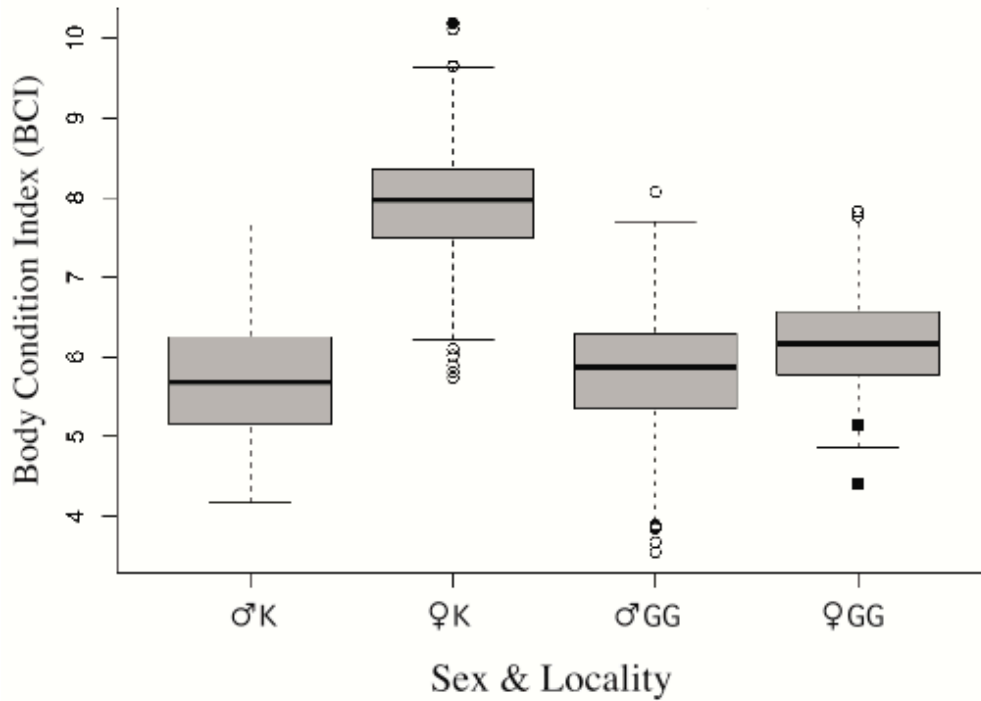


FIGURE 10. Quartiles and spread of model predictions based on the best-fitted model describing variation in body condition indices (BCIs) among Golem Grad Island (GG) and Konjsko village (K) adult male and female Hermann's tortoises. Filled circle (Konjsko) and squares (Golem Grad; square at value 4.7 represents two individuals) represent the four dissected females from Table 3.

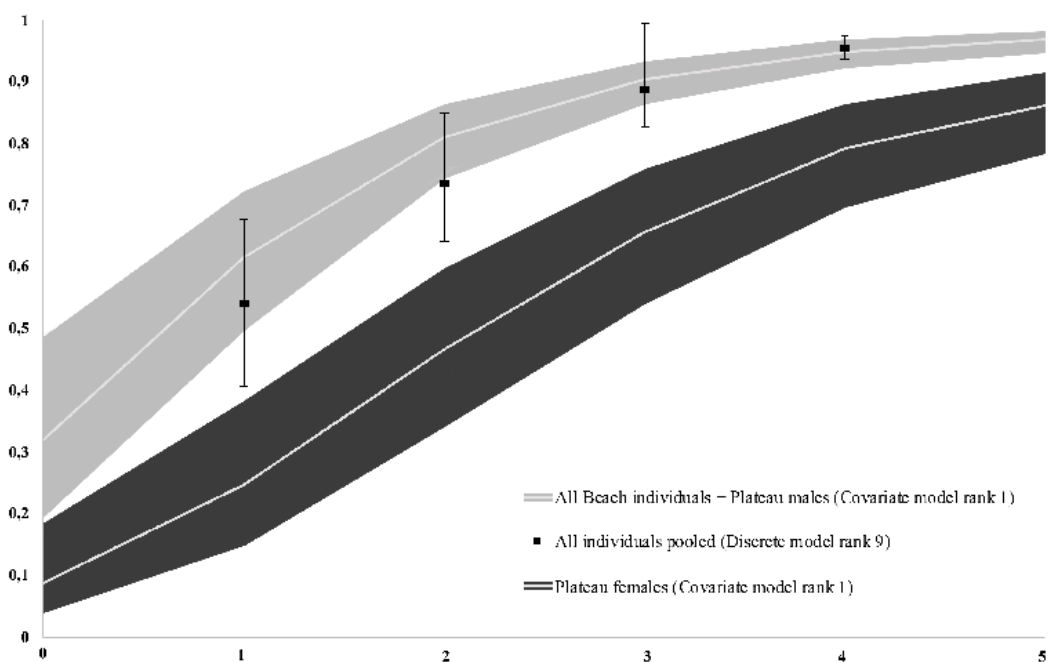


FIGURE 11. Estimated age-specific mean survival probabilities and 95% CIs of young Hermann's tortoises from Golem Grad Island, Macedonia obtained from a discrete model (Model rank 9, Table 6, p. 25), superimposed against the estimates and 95% confidence spread of mean age-specific survival probabilities 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 6, p. 26).

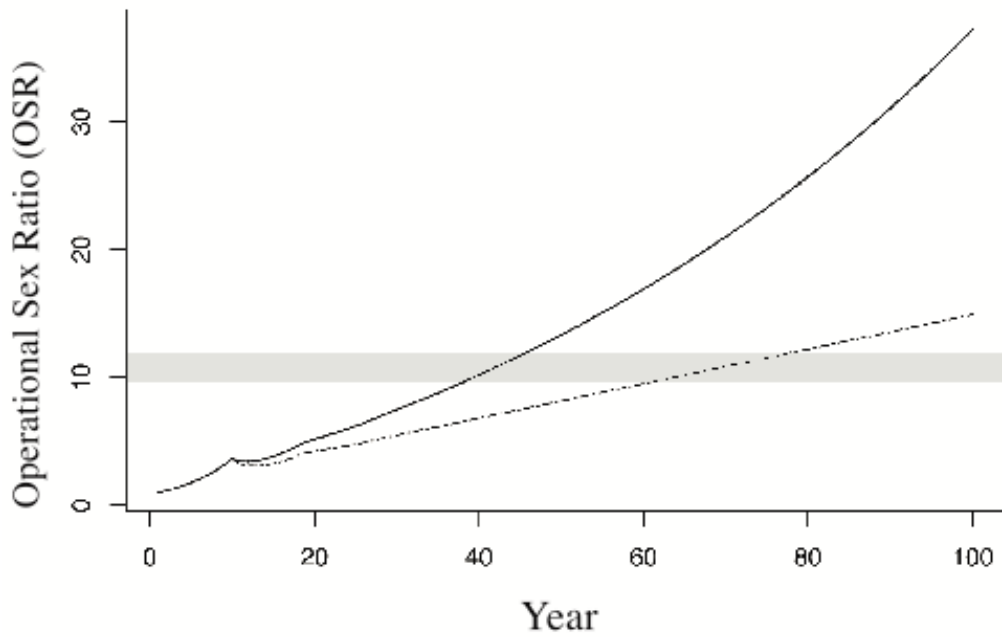


FIGURE 12. Simulated adult OSRs from projection matrices based on age- and sex-specific survival estimates from Golem Grad Island (section 3.3.2); thick grey line represents current island OSR estimate (\pm CI). Simulations differed in initial age of sex differences in survival: at eight years-old – full line; at 10 years-old – dashed line.

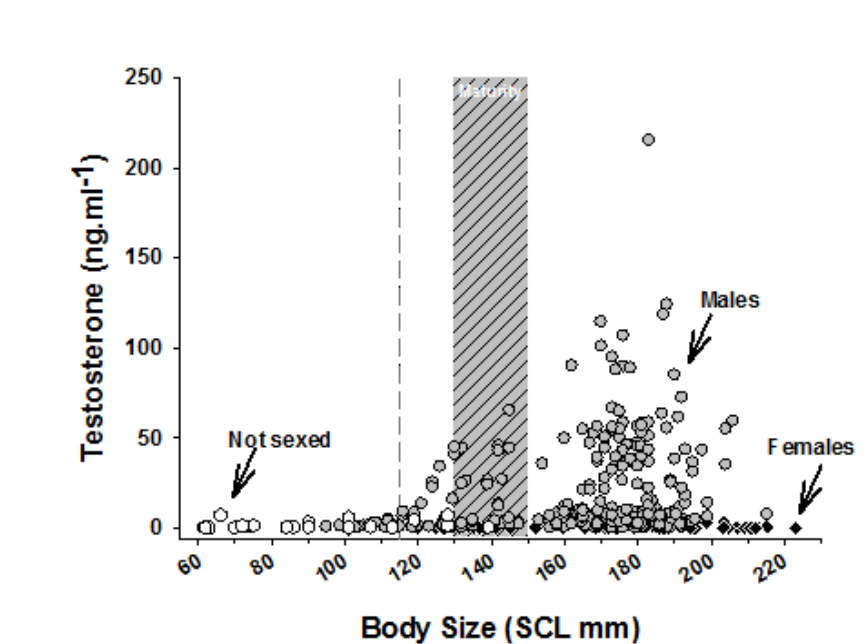
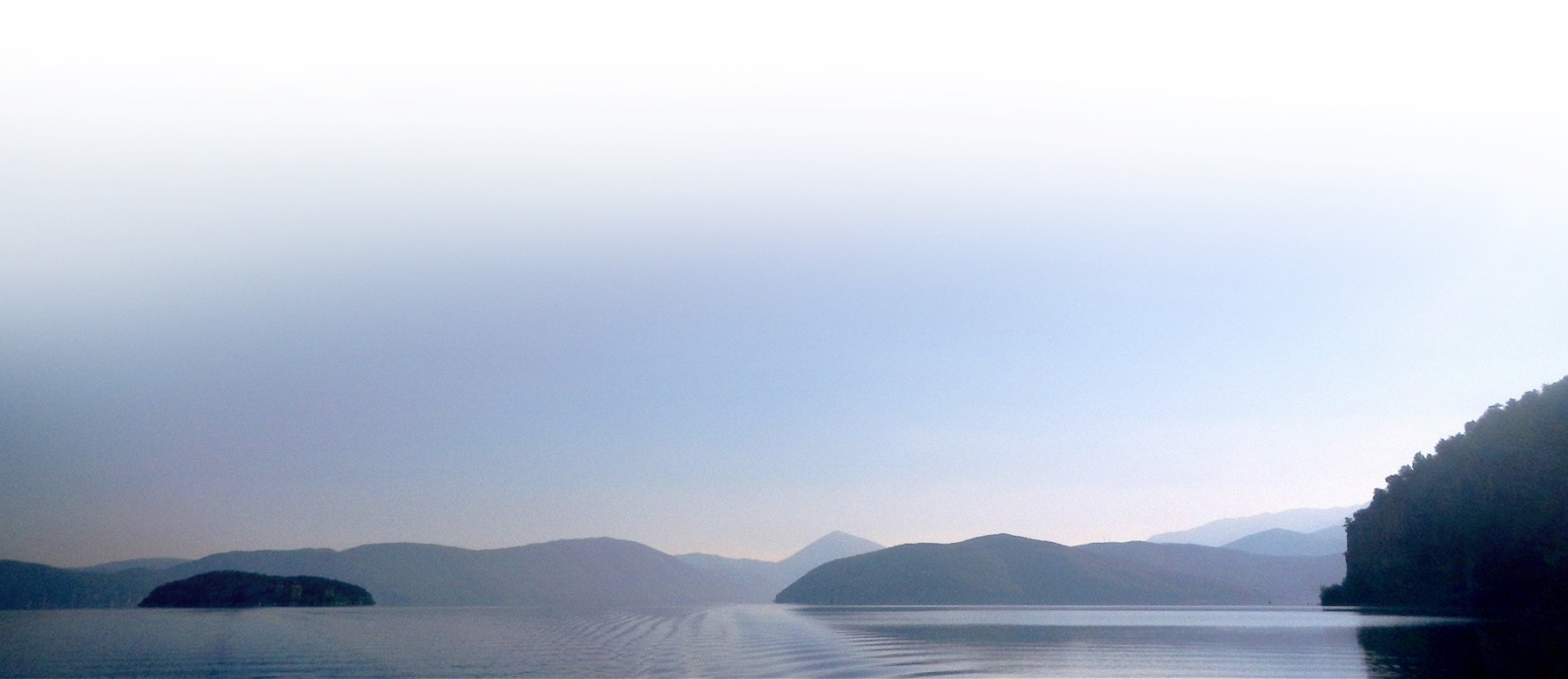


FIGURE 13. Plasma testosterone (T) levels of Hermann’s tortoises from Golem Grad Island before maturity (< 130mm SCL), at its onset (range of body sizes marked by the grey striped area according to literature), and after (> 150mm SCL). Empty circles are unsexed supposedly juveniles, grey circles are males and dark rhombi are females. Sexing occurred at point of plasma extraction or *a posteriori*. Dashed line represents the point at first T level increase from the baseline in males.

**5. RUN-OF-THE-MILL ECOLOGY: ISLANDS
AS FACILITATORS OF BIOLOGICAL
INSIGHT ENQUIRY**



While the first chapter was very personal and written in first person singular and the results were presented in the third person, the collaborative nature of the work to follow can only properly be presented in first person plural and so it is. Writing the following work has seen the help of numerous field assistants, data and analyses collaborators, idea refinement debates, constructive anonymous reviewers etc., some of which are dully stated as authors and coauthors of the chapters.

**5.1 WHEN CARAPACE GOVERNS SIZE: VARIATION AMONG AGE CLASSES
AND INDIVIDUALS IN A FREE-RANGING ECTOTHERM WITH DELAYED
MATURITY**

[2018, *Oecologia* 186: 953-963, Arsovski D, Tomović Lj, Golubović A, Nikolić S, Sterijovski B, Ballouard J-M, Bonnet X]

Growth rate during early life is a major determinant of adult body size, especially in species with delayed maturity (Stearns 1992; Madsen & Shine 2000); body size, in turn, has ubiquitous impacts on life history traits (Peters 1983). Selective forces that control variation in body size (VBS) over time are omnipresent. VBS at birth (static heterogeneity) can either be countered by compensatory effects of growth, or fuelled by the cumulative effects of the environment and create “dynamic heterogeneity” (Tuljapurkar et al. 2009). The constant face-off between these effects can generate cohort VBS, and theory suggests that longer generation times should correlate with lower initial VBS and a faster decline throughout life and vice versa (Gaillard & Yoccoz 2003); ungulates neatly follow this rule (Hamel et al. 2016). Consequently, in the pursuit to better understand growth variation and VBS, accurate descriptions of (individual/cohort) growth curve shapes are necessary, and prolonged immaturity mandates that they rely on large datasets that include long-term monitoring of individuals across all age classes. Alas, immature individuals tend to escape observation (Paradis et al. 1993; Pike et al. 2008), precluding detailed descriptions of (individual) juvenile growth curves. In long-lived species with delayed maturity, complex, species-specific juvenile growth curves have only been obtained from humans, few mammal species in captivity (Setchell et al. 2001), and sea turtles (Chaloupka and Zug 1997; Chaloupka 1998). In humans, although growth is not yet fully characterized (Gliozzi et al. 2012), there are two periods of accelerated growth that occur, respectively, after birth and several years later during adolescence (Davenport 1926; Leigh 1996). A very different pattern was observed in laboratory rats where growth rate progressively rises after birth and then exhibits a gradual decline prior to maturity (Hughes & Tanner 1970). Sea turtles display two growth spurts taking place just after birth and then a few years later. This is the only example from free-ranging animals, yet it is based on relatively small and sparse samples

and indirect skeletochronological ageing techniques, and should thus be considered with care (Chaloupka and Zug 1997; Chaloupka 1998). Nonetheless, differences in growth curve shapes, driven by variation of critical period(s), may well be species specific, and should be scrutinized.

Substantial perturbations occurring during critical phases of rapid growth are expected to have a strong definitive impact on adult size (Roselló-Díez and Joyner 2015). Multiple interactions between the sexes, the genes, and the environment mediated by complex physiological regulations underpin the resulting inter-individual (or between cohorts and inter-population) variability in growth rate (Badyaev 2002; Lui & Baron 2011; Roselló-Díez & Joyner 2015). Lummaa & Clutton-Brock (2002) reported various negative effects of unfavourable conditions (e.g. nutritional stress) during early development on many human adult traits. Nevertheless, the expected impact on adult body size was less documented. Overall the possible influence of environmental factors on the most sensitive periods of juvenile growth is an open question in free-ranging animals.

Thus far, mark-recapture studies performed on free-ranging individuals belonging to different taxa have provided extremely valuable information (Dietz et al. 1994; Lenihan & Van Vuren 1996). However, in most cases the juvenile sample size was limited to few observations and precise analyses were hampered by long intervals between recaptures before maturity; only crude juvenile growth patterns were inferred. The paucity of data explains why usually a linear, or a simple asymptotic growth curve was extracted (Congdon & Loben Sels 1991; Dietz et al. 1994; Lenihan & Van Vuren 1996; Zug & Parham 1996; Beaupre et al. 1998; Dodd & Dreslik 2008; Scott et al. 2012; Rodríguez-Caro et al. 2013) and rapid ontogenic changes in growth velocity may have been missed. To our knowledge growth spurts have been directly identified from dense and continuous repeated records only in humans, captive primates and in industrially raised animals, only when the time elapsed between successive measurements was reduced (Jobling et al. 1994; Noy & Sklan 1997). Perhaps other taxa display effectively simpler growth patterns? - It would be remarkable to observe that the kinetic of growth exhibits complex patterns only in those species where juveniles have been intensively monitored through regular recaptures of known individuals.

Several reptile species combine delayed maturity, long life expectancy, and wide ranges of body sizes (Andrews 1982; Stearns 1984; Dunham & Miles 1985; Berrigan & Charnov 1994). In these organisms, adult body size responds to environmental factors with cascading effects on most life history traits (Madsen & Shine 2000; Niewiarowski & Roosenburg 1993; Caley & Schwarzkopf 2004). Chelonians provide excellent examples of extremely delayed maturity that leaves plenty of room for complex growth trajectories to establish idiosyncratic routes during a prolonged and substantial increase in size. Immediately after hatching, individuals are naïve and must find appropriate resources. Exploring novel environments can defer growth. Indeed, small tortoises are extremely vulnerable and they must intensively use shelters, trading foraging for safety (Ballouard et al. 2013). Over time, the protective value of the shell increases and larger, more experienced immature individuals can escape predation more easily. A shift in their time budget may promote foraging and exploitation of thermal resources, potentially accelerating growth and increasing VBS. Yet, other factors like dispersal or ontogenic changes in their diets may blur or invalidate this scenario. Thus far, field studies have described simple patterns for most chelonians, but they were based on limited numbers of infrequent recaptures (Congdon & Loben Sels 1991; Zug et al. 1995; Zug & Parham 1996; Hailey & Coulson 1999; Lagarde et al. 2001; Dodd & Dreslik 2008; Živkov et al. 2009; Scott et al. 2012). Applying the necessary growth function can reveal a more realistic complex growth pattern even on small datasets [see Chaloupka's (1998) reanalysis of Zug et al.'s (1995) dataset]. However, in the lack of validation from a CMR framework, results based on indirect skeletochronological ageing techniques on limited data can be questionable. Clearly, accurate field data based on abundant and frequent recaptures are required to further explore these issues.

Juveniles are rarely captured and even less often recaptured, but we benefited from a favourable setting. The closed island system of Golem Grad



allowed us to accumulate and delve into a remarkably dense dataset of annual size measurements of free-ranging tortoises. Consequently, it was possible to combine frequent recaptures with data from annual growth rings (left) to obtain the age and growth of individuals. The long and non-uniform immature phase of long-lived chelonians likely reflects ecologically distinct phases of life. If humans experience accelerated growth immediately after birth

and then during adolescence (Davenport 1926; Leigh 1996), the fit of the S-shaped logistic growth curve we observed, suggests the opposite pattern for our tortoises: first, growth rate is slow, then it gradually increases, becoming more rapid in the intermediate class of juveniles, and later slows down before reaching asymptotic size (Tsoularis & Wallace 2002; p. 34, Fig. 8). From such results we could extrapolate that, 'in the lack of a mother's bosom', hatchling tortoises have only themselves to rely on. Fully independent neonates may require a 'grace period' during the first 500 days (~2.5 years; p. 34, Fig. 8) of life during which they gradually learn where to find key resources. Hatchling tortoises are small (estimated SCL_0 from both datasets ranges between 32.8 and 33.9 mm), possess a soft shell, and thus are vulnerable to environmental fluctuations or predators (Keller, Díaz-Paniagua & Andreu 1998; Barje et al. 2005). It is thus expected that they adopt a secretive life, foraging only when necessary; the systematically meagre representation of this demographic in other tortoise studies (e.g. Zug et al. 1995; Živkov et al. 2009; most localities in Willemsen and Hailey 1999) supports this notion. Strong ecological constraints along with morphological constraints on egg-size in chelonians (Macip-Ríos et al. 2013) translate into low

static heterogeneity illustrated in the tall and narrow bell curve of size distribution within the first year of tortoise life (p. 34, Fig. 7). Nevertheless, with size come safety and a harder carapace, thus successive acceleration of growth is imminent. An increase in VBS marks the first obvious departure towards dynamic heterogeneity, likely fuelled by individual differences in growth potential. This marks the onset of the second age cohort (two-four-year-old; p. 34, Fig. 7) during which compensatory effects seem to maintain the uniformity in VBS; smaller individuals are stimulated to exploit any available resources and compensate with faster growth to ensure survival, or they can likely selectively disappear (Plard et al. 2015). Between 60 and 70 mm of length (~600 GD/3.5 yrs) faster linear growth begins (p. 34, Fig. 8), likely supported by a firmer shell and familiarity with the environment. Subsequently, experience and boldness allow for more intense and possibly more efficient utilisation of environmental resources marking the onset of the last identified age cohort (≥ 5 -year-old; p. 34, Fig. 7) at which point dynamic heterogeneity seems to take over. This stage lasts a staggering ~8 years (1,400 GD; p. 34, Fig. 8) during which, a tortoise's more relaxed attitude towards its surroundings may lessen the constraints on size variation, promoting idiosyncratic growth trajectories. The wide range of estimated asymptotic sizes (162.8 ± 6.2 mm to 189.4 ± 6.4 mm) from bootstrapped datasets from the individuals of known age supports this idea. Meanwhile, opportunities, perturbations in the environment, or lack thereof, fuel individual variation in size progressively blurring the size distinctions between age classes - a notion well illustrated in Figure 7 (p. 34) by the progressive flattening and finally overlapping of bell curves between the ages of five and nine. This sudden progressive increase in VBS is surprising for an animal so low on the slow-fast continuum. Long-lived animals invest in survival rather than reproduction (Gaillard and Yoccoz 2003), so smaller more vulnerable individuals are under pressure to grow and catch up with their mates, thus continuously decreasing VBS. However, considering the delayed costs of compensatory growth (Metcalf & Monagan 2001), a chelonian's hardened carapace may well compensate for the survival benefits size would otherwise bring at an earlier age. In other words, the survival benefits of a hardened carapaces may give young and small (relative to

their age) tortoises the option of deterring possibly costly compensatory growth, thus promoting an increase in age-specific VBS. A marked increase in these tortoises' survival between the third and fifth year of age (p. 36, Fig. 11) remarkably corroborates this idea. Determinate growers, such as ungulates, pay the price in order to reach a safe size before growth ceases, therefore they experience an ever-decreasing VBS (Hamel et al. 2016). On the other hand, the Hermann's tortoise can grow significantly after maturity (p. 35, Fig. 9); accompanied by a solid carapace at the age of five this seems to translate into liberty in growth regimes regardless of maturity. In sea turtles, indirect skeletochronological ageing techniques suggested similar polyphasic growth before maturity, supposedly driven by diet shifts and changes in foraging areas (Chaloupka & Zug 1997; Chaloupka 1998). These results based on CMR data provide strong support to these pioneer studies and thus to the fact that complex patterns in chelonian growth before maturity might be more widespread than currently assumed. Aggregating immature individuals and thus neglecting possible rapid non-linear developmental shifts may result with major imprecision when studying the fitness consequences of early life variations. The elusive nature of immature individuals should promote a more systematic approach; for example, in reptiles artificial shelters and/or specific searching sessions bolster the detection of otherwise uncatchable juveniles (Bonnet et al. 1999, 2014; Ballouard et al. 2013). Precisely on Golem Grad most very small tortoises were found sheltered under stones while larger individuals were found using the classical visual searching technique.

Between the ages of nine-20 years, annual growth rate decreases markedly (p. 34, Fig. 8) and becomes negligible as observed in other populations (Bertolero et al. 2011). Supposedly this sharp decrease leaves little room for subsequent growth to contribute to individual variation in maximal body size. Willemsen and Hailey (1999) argued that the duration of growth before it decelerates is the only proximate cause of variation in adult size. The SCL range (155.5–218.2 mm) of the oldest individuals (characterized by smooth shells, presumably more than 25 years old; close to asymptotic size) should thus be projections of the spectrum of tortoise sizes at their respective times when growth had decelerated. However,

not all adults in our population seem to fully conform to this scenario. Figure 9 (p. 35) demonstrates that adult tortoises display a wide range of growth trajectories relatively independently from their body size at first capture. In other words, despite a reduced growth rate, substantial individual variations can be measured in adult tortoises, providing that large sample sizes are continuously monitored on the long-term (e.g. 5-10 years). Overall, the duration of growth before it decelerates is a crucial proximal cause of variation in size; however later interactions between genes and the environment during the long mature life of tortoises may well significantly influence asymptotic size.

Further disentangling the respective contributions of various growth rates before and after maturity on individual size is not easy, but it might be crucial to better understand the actual extensive range of body sizes found in many long-lived ectothermic species (Gotthard 2001). This is an important issue because body size influences many life history traits: for example, mating success during ritual fights in males (Willemsen & Hailey 1999) or fecundity in females (Andersson 1994, Lagarde et al. 2001). On the other hand, selective advantages of smaller size may maintain variation: early maturing small individuals may invest more resources into reproduction rather than growth, thereby balancing the advantage of a large body size (Stearns and Koella 1986). Additionally, variations in foraging resources may influence the opportunity for individuals to express their own growing potential (Gotthard 2001).

Finally, there is no dearth in reptile growth studies, and for a big part our data conforms to existing knowledge. Nevertheless, it has become evident that major gaps still exist, particularly when studying the long immature phase of reptiles with delayed maturity. The complexities that have been pin pointed in this study surely penetrate even deeper into the specific life history characteristics of this phase. Possible consequences on variation in adult traits urge further exploration of interactions between environmental fluctuations and age-cohort peculiarities.

5.2 COVARIATES STREAMLINE AGE-SPECIFIC EARLY LIFE SURVIVAL

ESTIMATES OF TWO CHELONIAN SPECIES

[2018, J Zool In press, Arsovski D, Olivier A, Bonnet X, Drillholle S, Tomović Lj, Béchet A, Golubović A, Besnard A]

This paper deals with the age-survival relationship prior to maturity (or at its very onset) in two chelonian species (the European pond turtle [*Emys orbicularis*] and the Hermann's tortoise). The pond turtle dataset adds relevant comparative insight important to better grasp the results for the model species of this thesis (the Hermann's tortoise), thus instead of omitting these data, prior to the discussion I have inserted a brief description of the studied population of European pond turtle and its study site (Box 1).

Box 1 [European pond turtle population and study site] This terrapin inhabits a broad range of habitats across Europe, northern Africa and western 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 M. 2009).

During 16 years (1997-2012), a total sampling hand-capture effort of 598 hours and 6,158 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 Ficheux et al. 2015). Among these, 298 could be aged using growth-rings (Castanet J. 1988; Olivier A. 2002) for a total of 809 captures. Sex was assigned for sexually-dimorphic individuals followed by permanent notch marking on the carapace (Cagle F.R. 1939).

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 et al. 1985; Charnov 1990; Congdon et al. 1993; Congdon et al. 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 H. 2001), evaluating conservation priorities (Congdon et al. 1993; Heppel 1998; Enneson & Litzgus 2008) and estimating conservation efficiency (e.g. after reintroduction and/or head-starting in Heppel et al. 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 et al. 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 to 92% in juvenile Loggerhead turtles (Table 11). Much is likely a 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 11). Perhaps even more importantly, the plethora of methodological approaches (last column, Table 11) likely contributes largely to this variation (see also Pfaller et al. 2018).

TABLE 11. 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			
<i>T. h. hermanni</i>	Neonate: 0.39 +/- 0.10	19 years of CR, Cormack-Jolly-Seber (CJS) model	Fernández-Chacón et al. 2011
	1-year-old: 0.45 +/- 0.08		
	2-year-old: 0.77 +/- 0.08		
	3-year-old: 0.68 +/- 0.07		
	4-year-old: 0.86 +/- 0.06		
	5-year-old: 0.88 +/- 0.05		
<i>T. h. hermanni</i>	Neonate: 0.54	14 years of CR, CJS model	Bertolero 2002
	1-2 years-old: 0.64		
	3-9 years-old: 0.91		
<i>T. h. hermanni</i>	0-2 years-old: 0.52	7 years of CR	Henry et al. 1999
	3-9 years-old: 0.88		
<i>Testudo graeca</i>	Neonate: 0.39	Thread trailing	Keller et al. 1998
<i>Gopherus polyphemus</i>	1-4 years-old: 0.45	/	Wilson, 1991
<i>Gopherus polyphemus</i>	Immature: 0.84 +/- 0.05	12 years of CR, CJS open population model	Tuberville et al. 2008
Freshwater Turtles			
<i>Emys orbicularis</i>	neonate: 0.02-0.08	7 years of CR, CJS model	Canessa et al. 2016
	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		
<i>Emys orbicularis</i>	neonate: 0.11	3 years of CR	Mitrus 2005
	1-year-old: 0.64		
<i>Emys orbicularis</i>	1-year-old: 0.53	/	Mitrus 2002

Species	Immature (age-specific) survival	Materials & Methods	Reference
<i>Emys orbicularis</i>	3-9 years-old: 0.80	/	Mitrus & Zemanek 2004
<i>Trachemys scripta</i>	Immature: 0.83	/	Frazer et al. 1990
<i>Myuchelys georgesii</i>	Immature: 0.58	/	Blamires et al. 2005
<i>Chelydra serpentina</i>	Immature: 0.75	/	Cunnington & Brooks 1996
<i>Chelydra serpentina</i>	Immature: 0.65 – 0.82	/	Congdon et al. 1994
<i>Chrysemys picta</i>	Immature: 0.81	/	Wilbur 1975
<i>Chrysemys picta</i>	Immature: 0.83	/	Mitchell 1988
<i>Emydoidea blandingii</i>	Immature: 0.78	/	Congdon et al. 1993
<i>Kinosternon flavescens</i>	Immature: 0.64	/	Iverson 1991
<i>Kinosternon subrubrum</i>	Immature: 0.72	/	Frazer et al. 1991
<i>Clemmys guttata</i>	Neonate: 0.81	30 years of CR, CJS model	Enneson & Litzgus 2008
Marine Turtles			
<i>Caretta caretta</i>	Immature: 0.72	Catch-curve analysis	Bjorndal et al. 2003a
<i>Caretta caretta</i>	Immature: 0.70	Catch-curve analysis	Frazer 1987
<i>Caretta caretta</i>	Immature: 0.89	Catch-curve analysis	Epperly et al. 2001
<i>Caretta caretta</i>	Immature: 0.83	CJS model	Heppell et al. 1996b
<i>Caretta caretta</i>	Immature: 0.86/0.92	CJS model	Chaloupka & Limpus 2002
<i>Chelonia mydas</i>	1-year-old: 0.91 +/- 0.03	23 years of CR, Burnham model	Bjorndal et al. 2003b
	2-year-old: 0.85 +/- 0.05		
	3-year-old: 0.91 +/- 0.04		
	4-year-old: 0.76 +/- 0.03		
<i>Chelonia mydas</i>	immature: 0.88/0.85	CJS model	Chaloupka & Limpus 2005
<i>Chelonia mydas</i>	immature: 0.83	13 years of CR, CJS model	Patrício et al. 2011
<i>Chelonia mydas</i>	immature: 0.88 +/- 0.02	9 years of CR, CJS model	Chaloupka & Limpus 2005

Here, a general analytical framework is presented 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). The approach was applied 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. 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 (Fernaández-Chacón 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 11), and robust age-specific analyses are lacking.

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 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 pond turtle (Fig. 14).

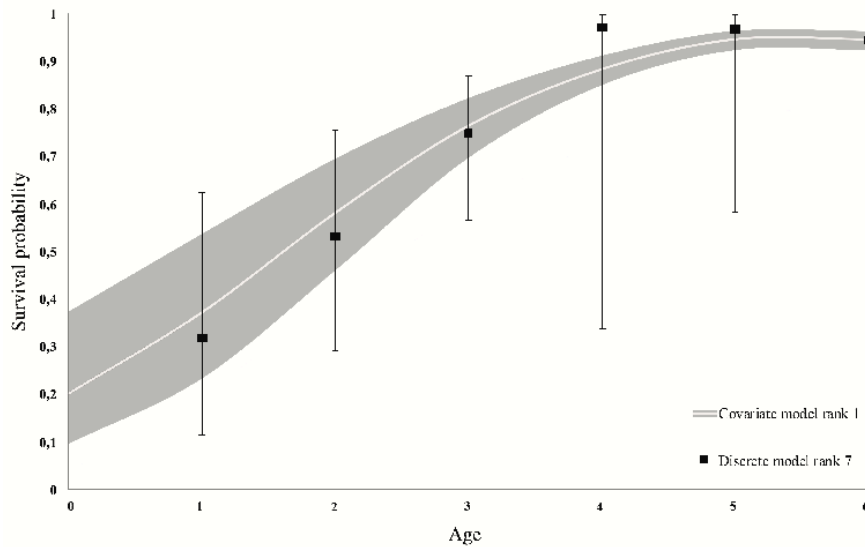


FIGURE 14. Estimated age-specific mean survival probabilities and 95% CIs of young European pond turtles from Camargue, France obtained from a discrete model (Model rank 7, Table 5 in Arsovski et al. 2018), superimposed against the estimates and 95% confidence spread of mean age-specific survival probabilities of the same population obtained from the best-fit covariate model (Model rank 1, Table 5 in Arsovski et al. 2018).

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. Due 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 11), 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 11) – mean survival is lowest in neonates, yet never below 20%, and it increases progressively with age (p. 36, Fig. 11; Fig. 14). 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 & Pärt 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], five 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 five-years-old (p. 36, Fig. 11; Fig. 14). 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 (Bertolero et al. 2011; Rogner 2009), 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 2000). 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. Our best-fit model implies significantly lower survival of younger females from this locality from birth (p. 36, Fig. 11). 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! This issue will be discussed at length in the following chapters.

The high variation in juvenile survival estimates that fail to give age or at least stage-specific estimates in Table 11 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 (p. 34, Fig. 7). 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).

5.3 APPROACHING TORTOISE MATURITY: A STORY OF MALE PHYSIOLOGY

Testosterone is a sex steroid that mediates sperm production, the expression of secondary sexual characters, and the functions that naturally follow – courtship and sexual behaviours (Nelson R.J. 2005). Pleiotropies (multiple targets) and complex regulations (trade-offs) often characterize hormones, and testosterone is no exception, decreasing immune functions and parental care in some species for instance (Ketterson & Nolan 1999, Folstad & Karter, 1992, Owen-Ashley et al. 2004). Thus, testosterone likely underlies important life-history trade-offs (Zera & Harshman 2001), making it a useful indicator of important sexual traits such as maturity in males.

Consequently, and remarkably, age-specific testosterone levels tell a story similar to the ones told by sexual behaviours. The smallest sexually active male (seen mounting another tortoise) on the island was 123.00 mm long (SCL) and Figure 13 (p. 37) suggests that testosterone levels start increasing at the very approach of 120mm SCL.



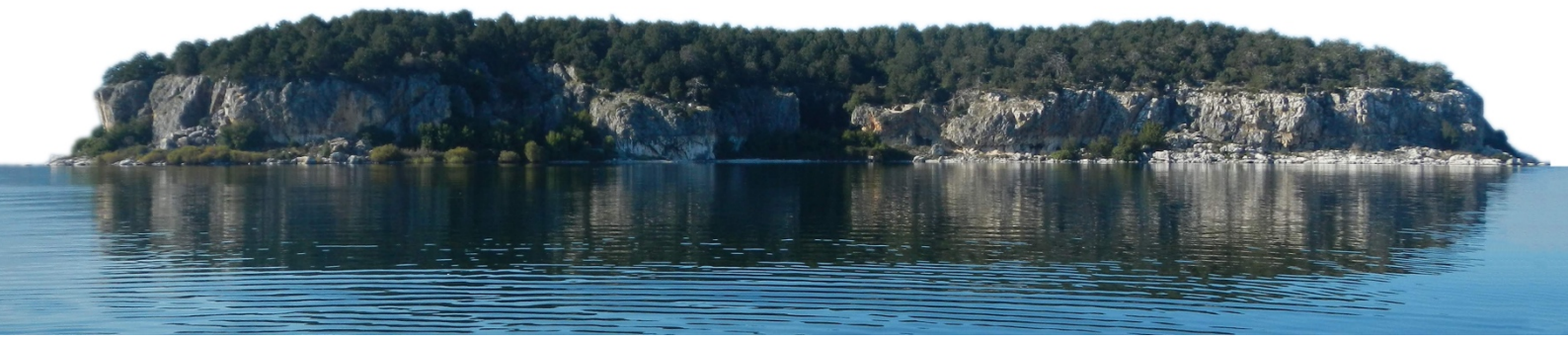
5.4 FIRST REFLECTION

- ON THE LIFE-HISTORY OF GOLEM GRAD HERMANN'S TORTOISES -

If I were to take previously discussed Golem Grad population-mean life-history estimates and write a short story extrapolating drawn conclusions into a species-wide reflection, the product would read: "Hermann's tortoises are armoured reptiles that hatch at a very small size (~30 - 40mm SCL, Fig. 8 & Table 10, pp. 34-35) with a shell not yet capable of providing the stiff safety that it will ultimately bring. This insecurity along with the absence of parental care has resulted with baby tortoises that are very wary of their surroundings and forage and explore only to acquire the bare resources for survival and growth, therefore only slowly picking up growth speed until two to three years old (Fig. 8, p. 34). This threshold is then marked with a sharp increase in the potential of age-specific body sizes (Fig.7, p. 34), likely facilitated by an acquired knowledge of the surrounding environment. Age-specific habitat-use and dispersal data would give even more support to these notions. Nevertheless, the soon to come survival-plateau (four to five years old, Fig. 11, p. 36) and an increase in growth speed (~800 GD [4.6 years], Fig. 8, p. 34) imply an acquired efficiency in obtaining resources and therefore efficient habitat use. This is likely supported by confidence gained from a finally hardened shell.

Male tortoises only reach maturity later at the size of ≥ 120 mm SCL (Fig. 8, p. 34), after at least few years of already living as a self-sufficient individual. Females supposedly reach this point at a larger size and presumably later (Bertolero et al. 2011). Hermann's tortoises do not seem to be in a rush to spend their resources on reproduction – perhaps a freedom that only comes with a very long life, or perhaps indeterminate growth. Since VBS is very high at this point, 120mm SCL should only be regarded as the minimal size-at-maturity, but certainly does not apply to every individual, species-wide. Some individuals are already 120mm long at seven years of age (Fig. 7, p. 34), whereas others either grow extremely slowly (with an asymptotic size of 150mm SCL, Fig 9, p. 35) or maintain a steady slow growth rate after maturity ($SCL_A > 200$ cm, Fig. 9, p. 35; largest reported Hermann's tortoise was 346mm long [Beshkov 1997])."

**6. FROM RUN-OF-THE-MILL TO OUT-OF-
THE-WAY: ISLANDS AS VECTORS OF
PECULIARITIES AND MEDIATORS OF
APPLIED RESEARCH**



The beauty of the amassment of ecological insight lies not only in attaining the power to extrapolate, but also in the little quirks and flukes that arise from big data and cannot easily find their place in current (at the time) general ecological laws. Golem Grad's Hermann's tortoises and their generous sharing of data in the sense of life trends, daily habits, variation in behaviour etc. continue to shed light on phenomena never before seen in this species, in turn leaving little room for rest to researchers' curiosities. The following chapters will try and make some sense out of the peculiarities that have arisen from dense biological data and moreover explore how such data can be applied to conservation biology.



6.1 A PRISON EFFECT IN A WILD POPULATION: A SCARCITY OF FEMALES INDUCES HOMOSEXUAL BEHAVIOURS IN MALES

[2016, *Behav Ecol* 27: 1206-1215, Bonnet X, Golubović A, Arsovski D, Djordjević S, Ballouard J-M, Sterijovski B, Ajić R, Barbraud X, Tomović Lj]

Due to their paradoxical consequences on reproduction, same-sex sexual behaviours (SSB) and their frequent occurrence in free-ranging animal species (from a wide array of lineages in Sommer and Vasey 2006; Bailey and Zuk 2009; Poiani 2010; Scharf and Martin 2013) have attracted generous research, particularly ultimate causes. Yet, there is a disbalance, little attention has been paid to nonadaptive hypotheses (Scharf and Martin 2013; for adaptive hypotheses see Camperio-Ciani et al. 2004; MacFarlane et al. 2007; Bailey and Zuk 2009; Bierbach et al. 2013; VanderLaan et al. 2014). Proximate causes, on the other hand, are likely technically difficult to investigate since SSB is often intermingled with other sexual behaviours, such as heterosexual behaviours (HSB) making it difficult to tease them apart and exclusively correlate SSB with physiological or genetic factors (for a rare example on snakes see Shine et al. 2000). It is nevertheless known that physiological factors (e.g. hormones) influence behaviours (Nelson 2005; Goldey and van Anders 2015) and by extension should likely influence SSB. Endocrinological experimental studies so far have explored sexual orientation through sex steroids (Poiani 2010; Goldey and van Anders 2015) and induced disorders (e.g., using knockout mice; Bakker et al. 2002, 2006) with deleterious repercussions such as hyper aggressiveness or behavioural asexuality, creating artificial behaviours unlikely to be favoured by sexual selection (Balthazart, et al. 1997). Nevertheless, empirical results suggest that male vertebrates that engage in SSB do not exhibit behavioural anomalies, are able to discriminate between the sexes, reproduce normally, and do not display unusual circulating testosterone levels (T) (Poiani 2010), thus insight from such experimental studies will likely be difficult to translate onto natural systems.

In captive animals, genetic, anatomical, neurophysiological, or hormonal investigations have failed to identify clear distinctions between the mechanisms that promote SSB versus HSB (Poiani 2010; Hoskins et al. 2015). Even in humans, one of the most intensively studied vertebrate species, the abundant efforts to

link sexual orientation with anatomy, physiology, and genetic mechanisms have revealed complex and equivocal patterns (Banks and Gartrell 1995; Rice et al. 1999; Zitzmann and Nieschlag 2001; Mustanski et al. 2002; Jannini et al. 2010). Although recent epidemiologic studies revealed that genetic factors influence human sexuality (Jannini et al. 2015), underlying genetic and physiological mechanisms of sexual orientation are not yet understood such that adaptive hypotheses remain controversial (Rahman 2005).

Golem Grad’s quasi-experimental natural situation allowed for the investigation of one of the main nonadaptive hypotheses reviewed by Bailey and Zuk (2009): The “prison effect” where “depriving individuals of members of the opposite sex causes them to engage in sexual interactions with members of the same sex.” This notion received support in a recent review on insects studied in captivity: The paucity of sexual partner (i.e., one sex kept in isolation) combined with high population density and exposure to sexual chemical stimulation is assumed to trigger SSB (Scharf and Martin 2013). However, comparable data are lacking in vertebrates or in natural populations. In the current study, a strong spatial and population contrast allowed us to explore the effect of environmental (female scarcity) and physiological (T levels) factors on the high SSB frequency exhibited by free-ranging males. Seven years of data from Golem Grad seem to point out to a scenario where SSB is triggered by specific environmental factors and where adaptive explanations play a limited role.

TABLE 12. Population density (number of individuals per hectare, D), numbers of adults sampled (N), and sex ratio (SR, adult males/ adult females) among 16 populations/sub-populations of *T. h. boettgeri* monitored in Greece (data from the Tables 2 and 3 in Hailey & Willemsen 2000) and in Macedonia (Golem Grad, Konjsko) and in three other species of *Testudo* (*T.h.h.*, JMB, unpublished; *T. horsfieldii*, Bonnet et al. 2001; Lagarde et al. 2002; *T. graeca*, Lagarde et al. 2008; XB, unpublished). SSB stands for same sex sexual behaviours that were observed in males only (expressed as % relative to all sexual behaviours recorded). The last column indicates the number of heterosexual behaviours (HSB) observed. Populations were ranked according to increasing density.

Species	Site	D	N	SR	SSB %	HSB
<i>T h. hermanni</i>	Callas	1.2	258	0.93	0	27
<i>T h. hermanni</i>	Saint Daumas	1.2	123	0.84	0	71
<i>T h. hermanni</i>	Lambert	1.6	64	1.21	0	4
<i>T. h. boettgeri</i>	Deskati	3.7	201	4.02	0	-
<i>T h. hermanni</i>	Redon	4.2	105	1.55	0	29

Species	Site	D	N	SR	SSB %	HSB
<i>T. h. boettgeri</i>	Mikra Volvi	4.6	338	3.69	0	-
<i>T. h. hermanni</i>	Riaux	5.2	78	1.69	0	27
<i>T. h. boettgeri</i>	Litochoron	5.3	102	2.09	0	-
<i>T. horsfieldii</i>	Bukhara	5.4	354	1.21	0	314
<i>T. h. boettgeri</i>	Langadia	5.9	71	0.55	0	-
<i>T. graeca</i>	Marrakech	5.9	192	1.21	0	192
<i>T. h. boettgeri</i>	Kilkis	11.3	99	2.81	0	-
<i>T. h. boettgeri</i>	Parga	12	187	0.83	0	-
<i>T. h. boettgeri</i>	Olympia	15.4	1,378	1.61	0	-
<i>T. h. boettgeri</i>	Kalamata	18.2	262	1.65	0	-
<i>T. h. boettgeri</i>	Agios Dimitrios	20	230	0.84	0	-
<i>T. h. boettgeri</i>	Konjsko	20	322	1	0	45
<i>T. h. boettgeri</i>	Meteora	20.2	4,855	1.9	0	-
<i>T. h. boettgeri</i>	Kastoria	20.5	265	1.85	0	-
<i>T. h. boettgeri</i>	Sparta	20.6	814	2.31	0	-
<i>T. h. boettgeri</i>	Igoumenitsa	39.6	237	6.41	0	-
<i>T. h. boettgeri</i>	Golem Grad Plateau	59.7	1,075	18.19	74	204
<i>T. h. boettgeri</i>	Golem Grad Beach	130	131	3.36	33	68

In free-ranging male Hermann's tortoises, high population densities combined with strongly male-biased SRs possibly generated a "prison effect" (Bailey and Zuk 2009) and SSB became more common than HSB in this situation only (Table 12). Hormonal investigations suggested that, not unlike other sexual behaviours, high expression of SSB correlated with high T levels. Remaining within the range of natural variations of T levels implies that SSB does not require specific adaptive or pathological explanations. In both the mainland and island populations, T levels were high in adult SA males, in accordance with the paradigm that androgenic steroids (e.g., T, 11-keto testosterone in fish) are primary stimulators of sexual activity in male vertebrates. Moreover, the most SA males (i.e., mating with females, engaged in SSB or combats, Figure 15) exhibited higher T levels, as observed in other reptiles (Aubret et al. 2002; King and Bowden 2013). Because an individual is not continuously SA, some of the "inactive" individuals monitored during random-focal blood sampling undoubtedly were SA animals that we observed between bouts of reproductive behaviour (especially in mainland tortoises where lower density decreases encounter rate). Nonetheless, we recorded higher T in males displaying the most vigorous behaviours: fighting or mounting other males. Therefore, this suggests

that the combination of high density and skewed SR led to frequent SSB in males, notably in individuals strongly stimulated by high T levels. External sexual stimuli (e.g., visual/chemical signals from conspecifics) can activate the brain structures involved in sexual arousal in adults (Arnold et al. 2002), high density promotes courtship behaviours in male tortoises (Hailey and Willemsen 2000), and T level correlates with sexual reactivity (Amstislavskaya and Popova 2004; Goldey and van Anders 2015). On Golem Grad, these factors were strongly amplified in males. Under strong sexual stimulation caused by multiple factors (high density + scarcity of females + high T levels), males attempted to copulate with the first encountered “partner,” generally females on the shoreline but more often with males on the plateau. A relatively similar behavioural “libido syndrome” where the occurrence of heterosexual courtships positively correlates with SSB has been described in captive cockroaches (Logue et al. 2009). Interestingly, libido scores also correlated with mating success, suggesting that selection for high heterosexual courtship intensity entailed nonadaptive SSB (Logue et al. 2009).

The studied population presents several exceptional characteristics and thus suffers from a lack of replication. Experiments where density and SR are manipulated are needed to gauge the validity of our conclusions. However, our results are based on a large sample size and long-term monitoring. Furthermore, the quasi-experimental shoreline/plateau situation of Golem Grad, along with the comparison with other populations belonging to different species (Table 12), offers support to the nonadaptive “prison effect” hypothesis (Bailey and Zuk 2009). Plateau-males and to a lesser extent shoreline-males can rarely find adult females, but instead encounter many male tortoises that morphologically resemble females while they are under T stimulation. Hyperstimulation and/or frustration created by a similar situation may promote frequent SSB as documented in feral-domestic cats (Yamane 2006). Deprivation of member(s) of the opposite sex generates sexual strain that can be relaxed by different behavioural outlets including onanism, SSB, or interspecific sexual behaviours (Exton et al. 2001; Yamane 2006; Sakaguchi et al. 2007). A positive impact of abstinence (a proxy of frustration) on both T levels and sexual motivation has

been documented in humans (Exton et al. 2001; Sakaguchi et al. 2007). Yet, nonadaptive SSB may simply reflect behavioural mistakes, such as inaccurate sexual partner discrimination (Scharf and Martin 2013). Although these explanations are not exclusive, the hypothesis that males cannot discriminate sex has been rejected experimentally (Galeotti et al. 2007). Many studies demonstrated the strong ability of tortoises, and of nonavian reptiles in general, to use chemical cues to distinguish sexual partner (Cooper and Pérez-Mellado 2002; Shine et al. 2003; Poschadel et al. 2006; Ibáñez et al. 2012). Overall, SSB may emerge and persist in natural populations because the costs for total SSB inhibition outweigh the costs of nonadaptive SSB (Thornhill and Alcock 1983; Burgevin et al. 2013; Scharf and Martin 2013; Engel et al. 2015). Mechanisms that eliminate SSB may negatively impact on HSB, for example, through a decrease of general sexual motivation if common neuroendocrine pathways are involved. Precisely, in vertebrates, T stimulates hypothalamic areas that promote both heterosexual and homosexual activity (Bakker et al. 2002, 2006). We speculate that the development, maintenance, and functioning of specific neuroendocrine structures that selectively filter out SSB might be too expensive (and useless) in male tortoises.



FIGURE 15. (B) A male mounting (+ vocalization) another male, himself mounting a juvenile male (left) (photographed by A.G.). (C) A male mounting a stone (centre) (photographed by A.G.). (D) A male mounting a female (right) (photographed by X.B.).

Other unusual sexual behaviours observed on Golem Grad Island, especially on the plateau, reinforce the notion that the most SA adult males deprived of females were highly stimulated (Fig. 15). Males (N = 12) were observed mounting juveniles, dead males, and tortoise skeletons (empty shells of males). Two were seen attempting to copulate with stones that vaguely resembled a tortoise (Fig. 15). In captivity, male SSB plus strange sex-toy behaviours have been reported in tortoises (Internet search using keywords

“tortoise and shoe”). These cases of juvenile mounting, homosexual Davian behaviours, skeletophilia (bellow), or petrophilia illustrate that the strong sexual motivation of males can overrule accurate discrimination of appropriate sexual partners. In the nearby mainland Konjsko population, in other Hermann’s tortoise populations, and in other *Testudo* species, uneven SR (generally unbiased or male biased) and varying population densities have been documented (Table 12). However, the combination of extremely skewed SR with very high population density and SSB was observed only on Golem Grad. We thus suggest that frequent SSB are expressed above a threshold that combines high density and skewed SR in physiologically predisposed individuals (e.g. male tortoises with high T levels).

Considering other adaptive or nonadaptive explanations does not change our main conclusions. For example, mate selection by females would reinforce the scarcity of partners for the males; the effect of practice (“Immature individuals learn ... through SSB”; Bailey and Zuk 2009) is unlikely in tortoises because sexual behaviours were never expressed by juveniles. The tortoises of Golem Grad provide the first documented example of a “prison effect” in free-ranging animals and thus offer a strong support to the hypothesis of nonadaptive causation for SSB. This finding suggests that proximate factors underlying SSB are not necessarily restricted to physiological disorders or require an adaptive basis (although indirect links between nonadaptive SSB and mating success exist; Logue et al. 2009). Under conditions with strong social stimulation and a scarcity of partner, SSB may be common.



6.2 SEXUALLY ABUSIVE TORTOISES DIGGING THEIR OWN GRAVE: SEX RATIO BIAS GENERATES INSUFFERABLE SEXUAL CONFLICT

[2018, *J Anim Ecol Under review*, Arsovski D, Tomović Lj, Golubović A, Besnard A, Trajčeska I, Bonnet X]

[2018, *Biol J Linnean Soc* 124: 394-402, Golubović A, Arsovski D, Tomović Lj, Bonnet X]

[2017, *Behav Ecol Sociobiol* 71: 93-100, Golubović A, Andjelković M, Arsovski D, Bonnet X Tomović Lj]

Sexual selection provides a unitary framework to study the tremendous variation in animal reproductive traits (Andersson & Iwasa 1996; Dall et al. 2006). The respective fitness interests of females and males are expressed through a continuum of mating strategies ranging from collaboration (convergent interests) to antagonism (divergent interests) between the sexes (Chapman et al. 2003). Strict monogamy characterized by tight cooperation between the sexes and strongly bonded pairs is rare (Bull 2000). In most species, males invest less in offspring production than females, generating predominantly divergent interests. Broadly, males can achieve forcible insemination via two main tactics with different evolutionary consequences (Clutton-Brock & Parker 1995; Holland & Rice 1998; Brennan & Prum 2012). When males are larger and stronger an evolutionary arms race of evolutionary forces between the sexes initiates the development of defensive attributes in females in order to lower mating costs (Arnqvist & Rowe 2002; Reinhardt et al. 2003; Muller et al. 2007; Johns et al. 2009; Hare et al. 2012; Lange et al. 2013; Michels et al. 2015; Peinert et al. 2016). When males cannot force insemination they usually harass females through a war of attrition (Clutton-Brock & Parker 1995) encouraging female defensive or escape behaviours, testing male quality and thereby optimizing sperm selection (Wang, Cummings & Krikpatrick 2015). Intermediate, cryptic coercive strategies and subtle female choices provide abundant exceptions and complications to this dichotomous view (Reyer et al. 1999; Pizzari & Birkhead 2000; Shine et al. 2003; Parker 2006; Knott et al. 2010). Yet, theoretical models and empirical studies converge on the idea that at least one sex (generally both sexes) loses substantial fitness benefits from forcible insemination to permit maintenance of the mating strategy (Parker 2006). This leads to a difference in optimal mating rates between the sexes generating sex-specific evolutionary interests termed sexual conflict (Parker 1979, 2006). If one sex imposes costs on the other, then we can easily

assume that the ratio of the sexes (the ratio of reproductively active males to active females in a given population at a given time – OSR [Emlen & Oring 1977]) could govern the asymmetries in the costs and benefits of mating i.e. has a profound impact on sexual selection (Kvarnemo & Ahnesjö 1996; Parker 1979). Namely, when the ratio of the sexes in conflict is biased in favour of the sex with higher optimal mating rates, the other sex experiences additional costs (Fitze & Le Galliard 2008; Le Galliard et al. 2005). Most literature on sexual conflict suggests that such bias should then be buffered with a control mechanism i.e. the sex in excess should experience higher selection pressure via intrasexual competition (Greenwood 1980; Wolff et al. 2002).

Recently, researchers have paid attention to the complex interactions between OSR, mating and breeding costs, that can drive sexual selection in previously unexpected directions (Fitze & Le Galliard 2008; Kokko & Johnstone 2002; Kokko & Monaghan 2001). This rings particularly true for sexually coercive mating systems where OSR bias can fuel sexual conflict by furthering the intersexual gap in optimal mating rates. For example, coercion can directly impact fitness through physical damage [e.g. to genitalia in garter snakes (Friesen et al. 2013), genital area in mosquito fish (Wang et al. 2015), cloacae in Hermann's tortoises (results; Hailey 1990), general wounding in some non-human primates (Smuts & Smuts 1993)], but also indirectly via the reduction of foraging rate (Magurran & Seghers 1994; Rowe 1994; Rubenstein 1986; Stone 1995), or even longevity of the harassed sex (Clutton-Brock & Langley 1997; Rowe 1994; Smuts & Smuts 1993; Westneat et al. 1990). Thus, while increasing sexual harassment promotes mating success, it can increase mating costs to the extent of preventing the harassed sex from reproducing at all, generating substantial costs to both sexes (Clutton-Brock & Langley 1997). Coincidentally, Smuts & Smuts (1993) proposed sexual coercion as a third form of sexual selection [alongside intrasexual competition and mate choice (Darwin 2009)]. Empirical studies on coercive mating systems have demonstrated how the force of sexual selection can be steered away from the prevalent sex by the interaction of (coercive) mating and breeding costs with OSR bias. For instance, Le Gaillard et al. (2005) as well as Fitze & Le Gaillard (2008) manipulated the OSRs of experimental viviparous

lizard population and observed that female mating costs increased with increased male bias up to the point of completely deterring females from mating and breeding. In this case male biased OSR does not only seem to lack self-regulatory mechanisms (e.g. male intrasexual competition), but can go so far as to progressively reduce female survival initiating what the authors have coined an 'extinction vortex'.

Elucidating OSR's influence on population viability is not straightforward however. This naturally imposes the question of the possible origins of such bias. In vertebrates, literature points to several options: (i) biases from birth, such as in species with environmental sex determination (Komdeur et al. 1997; Lolavar & Wyneken 2015; Pieau 1996), (ii) sex-specific juvenile survival rates (Bordier et al. 2014; Eberhart-Phillips et al. 2017; Veran & Beissinger 2009), (iii) sex-specific adult survival rates (Arendt et al. 2014; Le Galliard et al. 2005; Réale et al. 1996; Székely et al. 2014b), and (iv) sex-specific local emigration and immigration rates (Millert et al. 2011; Veran & Beissinger 2009). The causes of OSR bias are not consistent across taxa, and likely among populations. Properly untangling these possible sources requires comprehensive modelling, preferably in a natural population. This has only been achieved recently in a population of snowy plovers: adults exhibit a male biased OSR induced by male biased juvenile survival (Eberhart-Phillips et al. 2017). A result opposed to a comparative bird study where adult mortality rates were the main cause of OSR-bias (Székely et al. 2014a).

Studying the variety of possible underlying factors to OSR is crucial to better understand mating systems (Székely 2014a), population dynamics, and it may contribute to improve conservation policies (Bessa-Gomes et al. 2004; Veran & Beissinger 2009). Here, we examine the possible contributors and consequences of OSR bias in a very dense island population of Hermann's tortoises, a species with a polygamous and coercive mating system. Quantification of cloacae swollenness and injury levels between both localities (Fig. 16) and Hailey & Willemsen (2000) suggest possible female costs imposed by coercion under high population densities in this species, but to the best of our knowledge this has not been quantified. Using 10-year individual-based capture-

recapture (CR) data we modelled sex- and age-specific survival rates. To interpret the outcome, we used data on the environmental risks faced by tortoises (Golubović et al. 2013a), insight on the impact of OSR-bias on their sexual habits, growth and body size variation information of all age and sex cohorts along with abundant mortality records collected in the field. Finally, by superimposing such insight against comparable data from Konjsko we try to envisage the destiny of these confined, free-ranging, island tortoises: will sexual conflict generate a system where OSR-bias is continuously exacerbated (extinction vortex) or could it gradually be buffered?

Box 2 [Shift of harassment tactic] In tortoises, males occasionally court small immature individuals (Hailey & Loumbourdis 1990). Intensive harassment can result in substantial wounds. Females from the two studied populations were under different courtship pressures. At Konjsko, injuries were typically more frequent in larger individuals and were never observed in females smaller than 170 mm SCL and 17 years old or younger (age estimated from Fig. 8 [p. 34]). Thus, intensive coercive mating was concentrated on large females at least 5 years after maturity, revealing an important buffer age-span preventing harassment of small, possibly immature females. Conversely, small females on Golem Grad Island were often wounded long before they reached adulthood (p. 36, Fig. 11), revealing a lack of body size threshold. The smallest wounded females on Golem Grad Island were estimated to be only 8 years old (Fig. 16 according to Fig. 8 [p. 34]). The high population density and strongly male-biased sex ratio on Golem Grad triggers unusually intensive reproductive activity in males. Frustrated males not only court and mount females, but also other males (including immatures), dead tortoises, empty shells and even stones (Fig. 15). These behaviours have not been recorded in other free-ranging tortoise populations (Table 12). Consequently, a very high population density and skewed OSR not only increase the likelihood that a female will be courted, but also induce a behavioural shift in male mating tactics. This shift toward immature females may entail costs but cannot generate any benefit; in this case coercive mating was maladaptive.

The origin of OSR bias was explored comprehensively, eliminating potential contributors in a step-wise manner: i) even early-life sex-ratios (p. 26, Table 7), ii) absence of sex-specific early-life survival (p. 36, Fig. 11) and iii) lack of immigration and emigration (from the island), iv) unravel the significant difference in adult survival of the sexes as the sole, albeit sufficient contributor. Perhaps we will never know how this survival gap initially came to be, but projection matrices demonstrate that it alone can swiftly bring about the current OSR-bias, initiating a vicious demographic cycle (p. 37, Fig. 12). It is important to note that young (neonate-to-nine year old) females from the Island Plateau express consistently lower survival probabilities than other young island tortoises (p. 36, Fig. 11) and Golem Grad males were observed to inflict injuries to even immature females as young as eight years old (Fig. 16). Whether very young females truly also suffer lower survival on the plateau, or that is imposed by the model is still not clear due to their low sample sizes. Nonetheless, at least on the Island Plateau [only 5% of the population is female], sexual coercion on Golem Grad maladaptively targets even immature females, or those at the onset of maturity (p. 36, Fig. 11; Fig. 16). Therefore, besides not recognizing juvenile sex-specific survival as a strong contributor to OSR-bias, we acknowledge that for some females, pressures from male sexual assaults likely start before maturity, further exacerbating the trend.

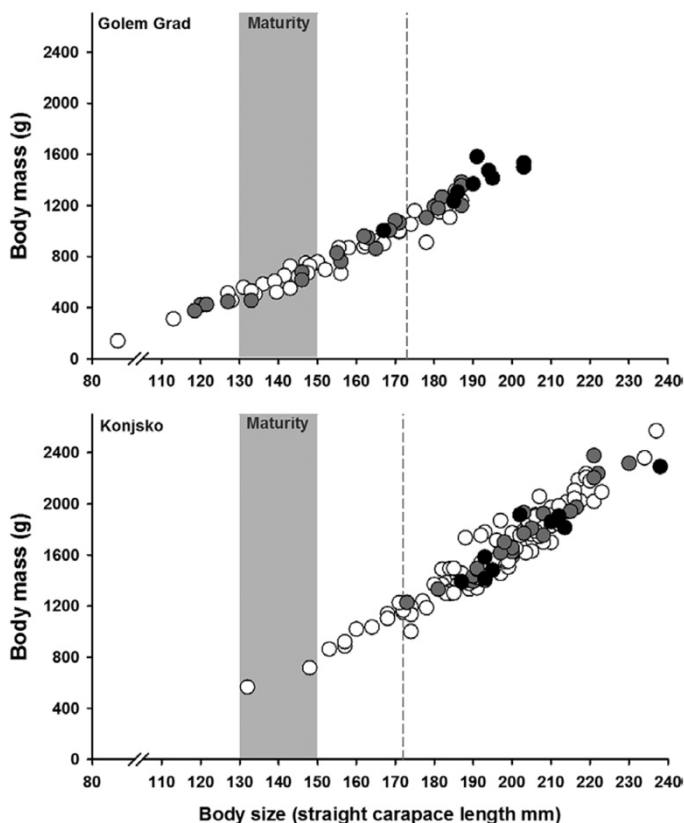


FIGURE 16. Relationship between cloacal injury level (white, grey, black pattern) as a function of body mass (y-axis) and body size (x-axis) recorded in two populations of free-ranging tortoises (total sample N = 208): Golem Grad (upper panel, N = 69) and Konjsko (lower panel, N = 139). For clarity, only three broad categories of injury levels are displayed: open circles for females without or with moderate injury (0-0.5), grey for average level (1) and black for strong injuries (1.5-2). The grey area indicates the range of body sizes at which maturity occurs in this species. The dashed vertical line, which indicates the minimal size for average injury level recorded in Konjsko females, facilitates comparisons between the two populations.

The reproductive input of female tortoises is likely more demanding in terms of resources (e.g. for vitellogenesis) than male input (Congdon et al. 1982), leading to sex-specific differences in optimal mating rates and sexual conflict (Parker 1979). Conflict could be exacerbated under high density (Blyth & Gilburn 2006; Cordero 1999) in Hermann's tortoises, since density promotes intensive courtship in this promiscuous reptile (Bertolero et al. 2011). Unsurprisingly, 96.55 ± 1.74 males/ha on Golem Grad trigger relentless eagerness to mate; this phenomenon is expressed to such extremes on the island that males also mount other males, dead individuals, empty carapaces, stones, etc. (Fig. 15). Conversely, sparse island females (8.88 ± 0.85 females/ha) offer little chance for male sexual coercion to diffuse, thus leaving little room to female mate choice. OSR-bias can steer selective forces from intersexual mate choice to strong intrasexual competition (e.g. male combats) that should eventually buffer the bias (Greenwood 1980; Kvarnemo & Ahnesjö 1996; Wolff et al. 2002). However, male survival is high on Golem Grad and combats occur relatively rarely (Table 5 in the appendix). Thus, where island male tortoises seem eager to eat and mate, lower female recapture probabilities suggest prudence when foraging to survive, likely in an attempt to avoid sexually charged males – apparently also a matter of survival.

Life-history trait estimates on Golem Grad seemingly point towards a scenario more to the likes of the experiments of Le Galliard et al. (2005) and Fitze & Le Galliard (2008) where sexual coercion increases female mating costs substantially, reducing or even hampering reproduction and initiating an 'extinction vortex'. Indeed, island female survival is significantly lower (0.84, CI 0.80-0.87 vs. 0.97, CI 0.96-0.98) and the few female dissections suggest a drastic difference in reproductive state between localities – island females with empty oviducts and only small follicles in the ovaries and a mainland female full of eggs and follicles of all sizes (pp. 20-21, Fig. 3 & Table 3). The constant low proportion of body reserves in all individuals (dissected males also had low fat reserves [0.0-0.3%, N=9, unpublished data]) alongside higher proportions of eggs and follicles (p. 21, Table 3), infer that variation in tortoise BCI is strongly influenced by

variation in reproductive state (in females) rather than body reserves. Dissected island female BCIs are within or beyond the lower quartile of island female BCIs (p. 36, Fig. 10) suggesting our non-random dissection sample consists of worst-affected females. Nevertheless, Golem Grad female BCIs are indistinguishable from those of the males of either population [females of the *Testudo* genus are the larger and heavier sex (Bonnet et al. 2001; Willemsen & Hailey 2002)], suggesting



that other island females might still breed, but are likely not very fecund. Comparatively [to Konjsko and other Hermann's tortoise populations (Bertolero et al. 2011; Djordjević et al. 2011)] small female body sizes on Golem Grad that never reach estimated larger sex-specific asymptotic size imply all adult females on Golem Grad are relatively recent recruits. Most island females do not seem to live and grow out their full potentials, and the

fate of the last dissected female on the island embodies this unfortunate scenario: female GG 3 (p. 21, Table 3) was found surrounded by nine males with an extremely injured and swollen cloaca (above) and too exhausted to escape their persistent coercive mating attempts. She was rescued, gently force-fed (sugar + water) and kept away from males, but nevertheless died two days later.

As for the females that manage to survive, other perils await – steep and high island cliffs. Golem Grad tortoises are more prone to risk taking behaviour (i.e. taking the plunge) than conspecifics from Konjsko (Golubović et al. 2013a). In our experiment,



FIGURE 17. Three individuals that had fallen from the cliff on Golem Grad island and suffered considerable damage on their carapaces. Top individual was already dead at point of encounter. Bottom individuals were found alive. Bottom left individual (female) was found dead two months after the encounter.

island females approached the edge of the enclosure significantly more than Konjsko females and eventually took a “hazardous” (but only available) exit, even in the absence of coercion. Interestingly, these differences between localities disappeared when male coercion was present, yet no females from Konjsko made an exit without a push.

These experiments, supported by a significantly higher proportion of recovered female to male tortoise shells with cracked carapaces (out of all recovered shells), and four direct field observations (Fig. 17; Golubović et al. 2013a) attest to the unfortunate phenomenon of “jumping” females when cornered by coercive males on Golem Grad Island. Habitat characteristics influence locomotor performances in the Hermann’s tortoise (Golubović et al. 2017), but implied intersexual differences in hesitation time prior to a risky move (Golubović et al. 2013a) and the experimental effect of coercion on otherwise tamer Konjsko females, suggest that this force has likely pushed the adventurous island behaviour a step further in females.

Unfortunately for this population, it is not only mean annual survival that has taken the toll, but also the temporal variation of this trait. In long-lived animals, survival variation should be canalized (Gould & Nichols 1998) against environmental variation, thus ensuring population growth even in

suboptimal conditions (Gaillard & Yoccoz 2003). Male island tortoises neatly conform to this rule with a variance close to zero (CI 0.00-0.02), whereas significantly higher female variance of nine percent (CI 0.03-0.14) has likely succumbed to environmental pressure brought upon by male coercion making their fate unclear (e.g. in predictable vs. unpredictable environments in Cayuela et al. 2016).

Guided by scarce literature on the discussed population-intrinsic regulation mechanism (Hailey & Willemssen 2000; Le Galliard et al. 2005) we were fortunate enough to identify a natural population experiencing sexual selection under the steering wheel of OSR-bias and sexual coercion. Quantifying female costs via several life-history parameters and applying them to projection matrices we conclude that an 'extinction vortex' is likely imminent. Nevertheless, adult tortoises can linger for a long time even after the last female dies, whereas faster paced animals would have a much faster response making us question whether such demographic drifts are actually rare or the time window to witness them is sometimes very short. In lack of more insight, a likely scenario that caused this on Golem Grad Island is a recent arrival (unpublished genetic data) of these tortoises to the island with an OSR bias beyond the threshold that initiates a vortex in interaction with sexual coercion in this species; a random event could be equally likely. Regardless, in a globally changing climate, environmental sex-determination in the Hermann's tortoise (Pieau 1996) can easily make this island's OSR scenario a widespread occurrence (e.g. Jensen et al. 2018) imploring further research into the identification of OSR bias and density thresholds that make a tortoise population unsustainable.

6.3 SECOND REFLECTION

- TO LET IT BE OR TO PRESERVE -

Detailed life-history trait estimates and their variation in a population of tortoises from Golem Grad Island shed light on a slow, but ongoing extinction event, that could have otherwise been overlooked. Now comes the inevitable question: “should something be done to put this process to a halt and possibly reverse it?” Persistent SSB mating attempts have likely diluted sexual coercion from the few present females, but even so, OSR bias and density are clearly still passed the threshold that reduces female survival. Several potential activities that could ameliorate the situation come to mind: (i) lower OSR bias by removing males /adding females, (ii) reduce male coercive mating attempts (e.g. by chemically castrating them), or (iii) physically keep most males from reaching females and sexually not yet dimorphic immatures (e.g. by fencing them out). Exploring whether any attempt would increase female survival is an overwhelmingly exciting contemplation, but such meddling should not be taken lightly. If enough traction is to be received from local stakeholders (National Park, municipality and local residents), individual based monitoring should not only continue, but be done under even higher scrutiny. This way insight can be gained on the recuperation process from a thorough life-history perspective, and possible unwanted side-effects would be noted and taken care of in time.



LEFT. Some of the oldest (>25/30 years, possibly even around 50 years old; this species' longevity is still very questionable) tortoises (N>100) on the island have Arabic numbers engraved on their plastrons suggesting an organized introduction event. Earliest reliable verbal records of tortoises on Golem Grad date to the 80s, thus this hypothetical event must have happened during Yugoslavia. At the time the island laid in a strict military controlled border area making the lack of any written records or confessionals from local residents and the National Park of organized activities a complete mystery.

7. CONSERVATION IMPLICATIONS

WHY AN APPARENTLY PROSPEROUS SUBSPECIES NEEDS STRICT PROTECTION? THE CASE OF *TESTUDO HERMANNI BOETTGERI* FROM THE CENTRAL BALKANS

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The Hermann's tortoise is "Near Threatened" according to the IUCN Red List (assessed in 2004), but because its populations are in significant decline it is also regarded as close to qualifying for "Vulnerable" (van Dijk et al. 2004). The situation is made more complicated due to the existence of two recognized subspecies across its distribution range that have faced varying threat levels and therefore enjoy different protection statuses. Namely, the western nominotypic subspecies (*T. h. hermanni*) is regarded as one of the most threatened reptiles in Western Europe (van Dijk et al. 2014; Zenboudji et al. 2016; Badiane et al. 2017) and locally classified as "Endangered" in Spain, France and Italy (Luiselli et al. 2014; Vilardell-Bartino et al. 2015), as well as on the international level (European Reptile and Amphibian Specialist Group 1996). Rapid development in the west has massively contributed to its current condition, and at present day increasing threats in the Balkan Peninsula (e.g. Vujović et al. 2015) might bring about a similar fate to the eastern "cousin" (*T. h. boettgeri*). Long-lived species such as tortoises rely heavily on the survival of reproductive adults for population growth (Hailey 1990; Gaillard & Yoccoz 2003; Bertolero et al. 2011) and moderate persistent perturbations can imperceptibly influence adult survival. Often such pressures can only become obvious once the population has been brought to an irreversible tipping point (Jonsson and Ebenman 2001; Shoemaker et al. 2013; Badiane et al. 2017) – the reality of the western subspecies. The eastern Hermann's tortoise does not benefit from a strict conservation status and its populations seem healthy (can be easily found in large numbers in the field (Djordjević et al. 2013), but many might well be close or at a tipping point. Consequently, the IUCN states that "field assessments of conservation status are highly desirable" and several more relevant sources have been asking for the

upgrading of the conservation status of both subspecies (Rozyłowicz and Dobre 2010; Djordjević and Ljubisavljević 2015; van Dijk et al. 2004; Bertolero et al. 2011; Ljubisavljević et al. 2011, 2014).

Box 3 [Population Viability Analyses]

Population viability simulations are a relatively rigorous tool used in species conservation, offering insight into population dynamics with possible cascading effects on policy making [for another example on the Hermann's tortoise please see Hailey and Willemsen (2003)]. We plugged in actual field data (Table 13) and data from literature (Hailey and Loumbourdis 1988; Hailey 1990; Willemsen and Hailey 2003; Bertolero et al. 2011; Couturier et al. 2014) into the software VORTEX (version 10.1., Lacy and Pollak 2014) and established population baselines, after which we ran parallel simulations with appropriate site-specific threats. Simulations were run for 100 and 1,000 years and carrying capacities (K) were estimated by scaling populations against the very intensively surveyed population on Golem Grad Island. For more details on the methodology please see Nikolić et al. (2018).

Here, in addition to the two previously discussed populations three more central Balkan (Danilovgrad in Montenegro and Trstenik and Pčinja in Serbia, Table 13) populations are presented. Finally, Population Viability Analyses (Box 3) are used to evaluate extinction probabilities of each population in the presence and lack of potential threats in order to reassess the subspecies' conservation status according to IUCN criteria. All study sites differ in surveyed area, degree of urbanization, site protection status and identified (observed and/or reported) threats (Table 13).

In general, no 'normal' simulations predicted extinction, but when disturbances were applied the situation changed dramatically (Figure 18); for

longer elaborations of the results and graphical presentations of the PVAs of all five populations please see Nikolić et al. (2018). For Golem Grad, PVAs merely confirm the results of the previous chapter, but this peculiar population is not representative of Hermann's tortoises from the Balkans. Desirable tortoises from the peninsula are likely most heavily affected by the pet industry. Figure 18 demonstrates the unfortunate fate of a Serbian population if allowed harvest quota of adult individuals (200 every three years) are continuously reached. This figure can easily be applied to Konjsko and Golem Grad tortoises whose dense populations offer easy collection by poachers besides legal harvest not being allowed. Easy access from Western Europe, where most animals end up, make

this a huge problem (Ljubisavljević et al. 2011: overview in Table 13). Captive breeding programs, legal in Macedonia and Serbia exacerbate the issue, since farms easily act as platforms to obtain “legal permits” for the transportation of wild caught tortoises. Dealing with these issues, while still preserving their habitats and the mosaic structure of the landscapes still present in their Eastern range can thoroughly benefit the species (Livoreil 2009; Rozylowicz and Popescu 2013; Badiane et al. 2017). Making such endeavours a priority can best be achieved by assessing their legal status both locally and internationally. Demographic data and the assessment of threats suggest that locally the Hermann’s tortoise should be considered “strictly protected”, whereas according to IUCN *T. h. boettgeri* should internationally be classified as “Vulnerable”.

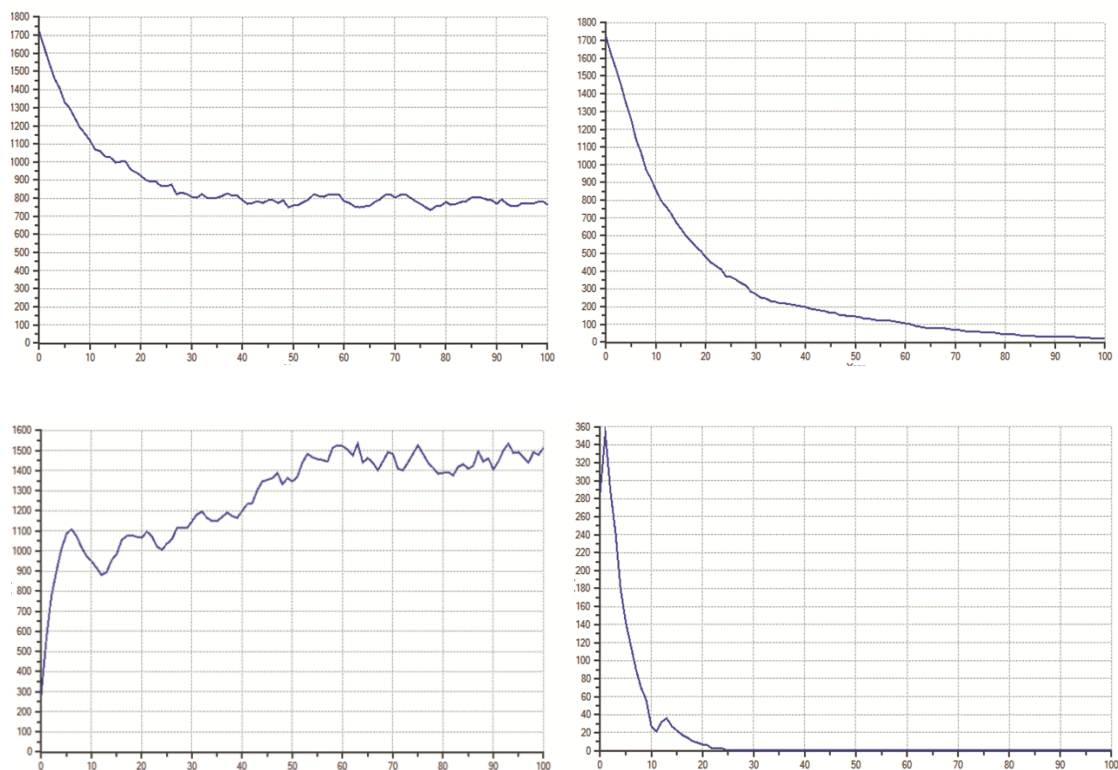


FIGURE 18. Select PVA simulation outcomes (y-axis: population size) over 100 years (x-axis: time) for Golem Grad Island (bottom) and Trstenik (top) under baseline circumstances (left) and with disturbances (right, legal harvest and increased female mortality in Trstenik and on Golem Grad, respectively)

TABLE 13. Basic characteristics of the five study sites of chapter 7 including: approximate surveyed area (ha), degree of urbanization, site protection status, identified (observed and/or reported) threats; crude survey effort.

Study site	Trstenik	Danilovgrad	Golem Grad Island	Pčinja River valley	Konjsko village
Approximate surveyed surface (ha)	25	4.3	20	25	15
Urbanization	Villages and weekend houses, arable land	Surrounded by motorway, arable land and settlement	Uninhabited, tourists	Weekend houses, gardens	Uninhabited village, tourists
Site protection status	None: sub-urban area	None: sub-urban area	Strictly protected area of a National Park	Landscape of Outstanding Features	National Park
Threats	Illegal collection, agriculture, vehicle collisions	Wildfires, vehicle collisions, urbanization	Closed population, male-biased sex ratio, increased female mortality	None recorded	None recorded
Search effort (person-days)	17 days, 2–4 people (51); 2009, 2011 and 2012	48 days, 1–5 people (144); 2010–2012	133 days, 4–17 people (1,330); 2008–2013	26 days, 4–10 people (182); 2008, 2009 and 2012	22 days, 4–8 people (132); 2010–2012

8. BROAD REFLECTION & RELEVANCE

It takes big effort and fortuity to reach even tiny moments of success when it comes to conservation based on fundamental research. I believe one such moment has arisen from this thesis – OSR and density are crucial to the success of populations of Hermann's tortoises. This should be taken most seriously by future reintroduction programs. In order to reach maximum efficiency in terms of survival and reproduction in the shortest time possible, high densities should be introduced carefully paying attention that OSR is at 0.5 (two females to each male) or perhaps even lower, and that no other conspecifics are already established in the area (Bertolero 2018). Besides Hermann's tortoises, this practice could likely benefit all other *Testudo* species, and probably also other animals with coercive mating rituals and a long life. As a species with temperature-dependent sex determination, the Hermann's tortoise is a convenient candidate for the successful and efficient implementation of such conservation advice via captive breeding programs. On another note, if harvest programs are impossible to ban in certain countries (legal in Serbia), they should at least be heavily controlled. Males should be the most exploited sex, but if possible, adults should altogether be avoided in such long-lived species.

Extracting knowledge from such examples can provide simpler conservation advices that are easy to follow, and offer more efficient resource spending, making conservation cheaper. Yet conservation today is neither cheap nor efficient. International organizations have invested huge amounts of resources in the developing (e.g. Macedonia) and third world in order to preserve biodiversity. The corrupt nature of most of these areas require a cascade of expensive international actors to implement projects. By the time resources reach implementers, such as field biologists, there is only a trickle of the original resources and surely not enough to promote long term studies and sound conservation. This system has promoted the artificial separation of research from conservation.

My own experiences getting resources to implement fundamental research have perhaps made me bitter. The incredible lengths one needs to go in order to justify research projects, such as insistently having to introduce the terms "saving", "conserving", "raising awareness" is discouraging to say the least – after all, no

conservation effort has ever “saved”, “conserved” or “raised awareness” in a matter of one year and several thousand euros. Fundamental research needs to become the new “awareness raising” or “saving” in conservation, and resources need to therefore be distributed to projects with long-term effects, rather than short-term good-on-paper plans.

Fortunately, systems such as Golem Grad Island offer easy collection of dense data that can in turn be put to good conservation use without preconceived notions. **Applied conservation should only be the inevitable and likely unavoidable side-effect of research, rather than a short term must!**

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1A. APPENDIX

1.1 Statistical Analyses

1.1.1 GROWTH

The following analyses incorporated data collected from Golem Grad island between 2008 and 2016 during 19 field sessions adding up to 169 search days. 13,115 recaptures were collected from 1,830 individuals. Growth patterns and asymptotic sizes were explored from two datasets: age at size data from relatively young (1-17 years old) aged individuals (see Box 1A), and incremental growth data from supposedly mature individuals (Bertolero et al. 2011) that measured ≥ 130 SCL (thereafter referred as individuals of known age vs. individuals of unknown age). Additionally, mean and maximum adult sex-specific body sizes of 268 males and 399 females from Konjsko were extracted.

1.1.1.1 Age-specific variation in body size (VBS)

The frequency distribution of individual SCLs for each of the first nine

Box 1A [Ageing] Recaptures of hatchlings over years provided an absolute age. In order to minimize possible error while ageing individuals from growth rings, one growth ring was considered to be deposited per year. Then, considering recaptures over years, each count was corrected following the most parsimonious approach (e.g. if an individual was captured in 2008, 2009 and 2015 and aged as 1, 2 and 7 years old, respectively, the last instance would be corrected to 8 instead of the first two). Very small, 1 to 3-year-old tortoises were easily aged. However, since counting became more ambiguous over time, when considering older individuals, only those that had been recaptured at least twice without significant discrepancies among estimated ages were retained. In practice, all the individuals where the error margin added up to more than 5 throughout all recaptures, were removed (2 instances only).

age classes was visually explored (pp. 16-17, Table 1 for the breakdown of used individuals and observations). The comparison between age-specific distribution curves of SCLs allowed for the detection of shifts in VBS among age cohorts, e.g. a lack of change in VBS would generate a succession of broadly identical curves, whereas a constant decrease/increase in VBS within the population would produce a progressive and regular change (e.g. linear/curvilinear). Since tortoises can reach maturity at various sizes (Willemsen and Hailey 1999) we assumed that VBS increases towards maturity and will generate successively flatter (wider and shorter) curves (unlike ungulates where VBS at maturity is very small [Hamel et al. 2016]). Whether such change is progressive, or

characterized by non-regular steps at crucial ages, creating sets of curves facing different ecological and/or genetic constraints, was an open question.

1.1.1.2 Population and cohort mean asymptotic sizes

Data obtained in individuals of known age were fit with both the Bertalanffy growth model [$SCL_t = SCL_A - ((SCL_A - SCL_0) e^{-kt})$] and with a logistic growth model [$SCL_t = SCL_A / (1 + e^{b-kt})$], whereas data obtained in individuals of unknown age were fit with Fabens' method of fitting the Bertalanffy growth model [$SCL_t = SCL_A - ((SCL_A - SCL_0) e^{-kt})$] (Fabens, 1965). In the equations above: SCL_A is the population mean asymptotic size, SCL_0 is length at time 0, SCL_1 and SCL_2 are observed straight carapace lengths in successive years, k is a growth rate constant and t is age in Growth Days (GD). The estimates of the growth constant k , SCL_A , and SCL_0 were obtained through an iterative non-linear regression in R v0.99.879 (R Core Team 2014), using our own data to find suitable start values for the non-linear model ($k=0.0005$, $SCL_A=220.0$ mm, $SCL_0=32.7$ mm). Even though SCL_0 is not a parameter in Fabens' method of fitting Bertalanffy's growth model, it could be estimated analytically as described in King et al. (2016), using SCL at birth (smallest individual captured on the island SCL = 32.7 mm) and $t = 146.3$ (the estimated GD needed to obtain 32.7 mm of SCL according to the best fit model of growth).

Since growth coincides with the period of active thermoregulation (Bertolero et al. 2005), we excluded hibernation from growth calculations. The onset and the end of hibernation were obtained in the field from 10 individuals fitted with temperature data loggers in late summer in 2010 and 2011 and recaptured the following spring (unpublished data). On average, the duration of hibernation was 190 days. We considered that the activity period elapsed from the 22nd of April to the 14th of October (175 days).

1.1.1.3 Individual variation in size and growth

The 'individuals of known age' dataset was randomly resampled 10,000 times using parametric bootstrapping and mean asymptotic size was estimated for each resample. Differences in asymptotic size between resamples would

likely be driven by shifts in individual trajectories from the original sample picked up more frequently by chance by the bootstrap procedure.

As for the individuals of unknown age, a smaller subsample of tortoises that had been encountered and measured during at least 5 consecutive years was used to build individual-based growth curves and estimate individual-based asymptotic SCLs. This way the population's full potential for growth variation could truly be appreciated. After sexual maturity Hermann's tortoise growth decreases linearly as a direct function of size, a pattern that fits well to Bertalanffy's model (Hailey & Coulson 1999). We therefore used Bertalanffy's growth model [$SCL_t = SCL_A - ((SCL_A - SCL_0) e^{-kt})$] where individual estimates of SCL_A were obtained through an iterative non-linear regression using the sex-specific value for the growth constant k (from the analyses of individuals of unknown age) as constrained value. The first capture occasion was treated as growth day zero, thus the estimate of SCL_0 represented the expected size of the individual at the day of first capture

1.1.2 BODY CONDITION

The following analyses were performed on all individuals with SCL >130mm from both localities. Each individual's body mass ratio to SCL (body condition index [BCI]) was extracted at each point of re/capture. Variation in BCI was modelled as a response to the variation in the additive and interactive effects of sex and locality. Each individual was encountered and measured 5.0 times on average on Golem Grad and 1.6 times in Konjsko. It is important to note that these measurements were distributed almost equally between seasons (spring [April and May] and summer [June, July and August]) and sexes: 3250 and 3448 males, and 233 and 206 females were encountered and processed during spring and summer months, respectively. In Konjsko, in the same respective order: 297, 325, 226 and 216 measurements were collected. Additionally, in order to account for pseudo-replication from repeated measurements, individuals were accounted for as a random factor in the generalized linear mixed models using the package 'nlme' (Pinheiro et al. 2017). Competitive models were ranked according to AIC (Burnham & Anderson, 2002). Finally, predictions based on the best-fitted model were made using the

'AICcmodavg' package (Mazerolle, 2011) and plotted in R v0.99.879 (R Core Team 2014).

1.1.2.1 Fecundity and mating costs

Recently dead individuals found in the field were carefully dissected. Female fecundity was noted by counting eggs in the oviducts and ovarian follicles of different sizes (0.5-1cm, 1-2cm and >2cm in diameter) in the ovaria. Taking into account the difficulty of estimating tortoise fecundity in lack of appropriate equipment (e.g. x-ray machine) and nest site location, this method provides precise data but very small not random sample sizes (no animals were sacrificed; Golem Grad $N[\text{♀}]=3$, Konjsko $N[\text{♀}]=1$) despite the long period of study. The proportions of both body fat and entire reproductive system (oviducts + ovaria + follicles and eggs) from total body mass were calculated for each individual.

1.1.3 SURVIVAL, POPULATION SIZE & SEX RATIO

Primarily goodness-of-fit tests were performed on the datasets based on the CJS model using U-CARE (Choquet et al. 2009a). All following survival analyses were performed in E-SURGE (Choquet et al. 2009b). The obtained capture probabilities from the best fit models, along with the raw numbers of individuals could be used to estimate population size, and/or cohort sizes (sex, age, sexual behavior etc.). Sex-specific population sizes were used to estimate sex-ratio among age classes as well as OSR. Parametric bootstrapping was used

1.1.3.1 Adult survival

Adult survival was estimated using CR histories of adult individuals (Bertolero et al. 2011) from Konjsko (complete CR dataset) and Golem Grad (1,309 individuals; 4,415 annual recaptures), separately, collected by 2017 and 2016, respectively. Multievent (Pradel 2005) mixture models (Pledger et al. 2003) combining live recaptures and dead recoveries (Schaub & Pradel 2004) were implemented in the software E-SURGE (Choquet et al. 2009b). Mixture models allow for recapture heterogeneity (by masking multiple heterogeneity states

under one field observation i.e. event), thus at first capture (initial departure state) individuals could be adult with high or low recapture probability ($A+$ and $A-$, respectively). They may then survive from year t to $t + 1$ (Table S1, matrix Φ) with probability $\phi^{A+/-}$ or they may move to a just-dead state (f) with probability $1 - \phi^{A+/-}$. Similar to other recovery models [e.g. (Schaub & Pradel 2004)], individuals whose empty shells were recovered moved to an absorbing long-dead state (RS). The states thus being $A+$, $A-$ and RS . The event matrix P (Table S1) defines events (field observations): 1 – not observed, 2 – observed as an adult living individual; this event masks both high and low recapture probabilities (p^{A+} and p^{A-} , respectively), and probability to be recovered as a dead tortoise shell (p^{RS}). From an initial model: Φ [sex*site], P [sex*site*het*t], we used a backwards selection procedure, retaining the best linear combination [lowest Akaike information criterion (AIC, Burnham & Anderson 2002)] first on recapture probability and then survival.

TABLE 1A. Elementary matrices: Φ (survival) estimating transition probabilities from t to $t + 1$ i.e. survival probabilities (ϕ). Once an individual's carapace has been recovered, during the following transition it can only transit into the unobservable dead state (f). Elementary matrix P estimating recapture probabilities: observed as an adult with high capture probability (p^{A+}), observed as an adult with low capture probability (p^{A-}), observed as a recovered carapace (p^{DR}).

	matrix Φ					matrix P				
	$A+$	$A-$	RC	f		NO	A	RC		
$A+$	(ϕ^{A+}	0	1-	0	$A+$	($1- p^{A+}$	p^{A+}	0
$A-$		0	ϕ^{A-}	1-	ϕ^{A+}	$A-$		$1- p^{A-}$	p^{A-}	0
RC		0	0	0	1	DR		$1-$	0	p^{DR}
f		0	0	0	1	f		p^{DR}	1	0

The model selection procedure entailed the dropping and addition of parameters starting with recapture probability and followed by survival, until a combination with the lowest AIC (Akaike information criterion) was found (Burnham & Anderson 2002). The initial model was: Φ [sex*site], P [sex*site*het*t].

1.1.3.2 Early-life age-specific survival

The following analyses were performed on field data collected between 2008 and 2016; during 19 field sessions adding up to 169 days, 1,225 recaptures were collected from 466 aged immature individuals (<130mm SCL). All of the individuals used in these analyses are present in the known-age growth dataset (pp. 16., Table 1); more individuals could be added to the survival analyses even if they hadn't been recaptured twice or more after using the growth model to ascertain their ages-at-capture via individual SCLs. All used tortoises were born between 1,999 and 2015; the chronological breakdown of captured animal numbers per birth year can be found in Table 2A.

TABLE 2A. Captured individuals of aged immature Hermann's tortoises per hatching year on Golem Grad.

Birth year	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
Captured individuals	7	10	16	14	34	36	41	44	64	87	48	12	5	19	15	7	7

Heterogeneity and sex uncertainty were dealt with using multievent model approaches (Pledger et al. 2003; Pradel 2005), thus sex was also coded as state, instead of group (as was in the adult survival dataset). The models were based on 9 underlying biological states denoting differences in sex, site and heterogeneity class (Table 3A).

TABLE 3A. Abbreviations (left column) and descriptions (right column) of states that one to nine years old Hermann's tortoises from Golem Grad can assume and transit among.

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

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 4A), dispersal between sites, given the individual survived (matrix Ψ , Table 4A), and change of recapture heterogeneity class given the individual survived and changed site (matrix F , Table 4A). 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 wouldn’t change recapture heterogeneity class). Nonetheless, since no tortoise changed site and all were visually searched for (instead of using traps which could promote change of recapture heterogeneity class) matrices Ψ and F were not parameterized. 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 4A), the other to estimate the probability of correctly sexing individuals (matrix S , Table 4A).

Estimating parameters between nine age classes, sexes, and sites requires very dense and large datasets in order to obtain robust and precise estimates. This dataset came very close to meeting these requirements. Nevertheless, only one individual was captured as one year old; covariates (linear, logarithmic and quadratic) were implemented on the age-survival relationship in order to obtain inestimable parameters and streamline estimates.

TABLE 4A. Elementary matrices: i) survival matrix Φ , f is the probability to survive from t to $t+1$; ii) dispersal matrix Ψ , ψ is the probability to be faithful to the site of first capture from t to $t+1$; iii) change of heterogeneity class matrix F , f is the probability of reaching the high recapture probability class; iv) first event matrix P , p is the probability of being recaptured, conditional on the departure states (Table 3A); v) second event matrix S , s is the probability to assess the sex of the individual, 0 – unobserved, 1 – observed as male on the Plateau, 2 – observed as female on the Plateau, 3 – observed as unsexable on the Plateau, 4 – observed as male on the Beach, 5 – observed as female on the Beach and 6 – observed as unsexable on the Beach.

$$\begin{array}{c}
 \text{i) matrix } \Phi \\
 \begin{array}{cccccccccc}
 & M1 & m1 & F1 & f1 & M2 & m2 & F2 & f2 & t \\
 M1 & \left(\begin{array}{cccccccccc}
 \phi & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi \\
 0 & \phi & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi \\
 0 & 0 & \phi & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi \\
 0 & 0 & 0 & \phi & 0 & 0 & 0 & 0 & 0 & 1-\phi \\
 0 & 0 & 0 & 0 & \phi & 0 & 0 & 0 & 0 & 1-\phi \\
 0 & 0 & 0 & 0 & 0 & \phi & 0 & 0 & 0 & 1-\phi \\
 0 & 0 & 0 & 0 & 0 & 0 & \phi & 0 & 0 & 1-\phi \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi & 0 & 1-\phi \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi & 1-\phi \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1
 \end{array} \right)
 \end{array}
 \end{array}$$

ii) 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- ψ	0	0	0	0	0	0	0	1- ϕ
m1	0	ψ	0	0	0	0	0	0	0	1- ψ	0	0	0	0	0	0	1- ϕ
F1	0	0	ψ	0	0	0	0	0	0	0	1- ψ	0	0	0	0	0	1- ϕ
f1	0	0	0	ψ	0	0	0	0	0	0	0	1- ψ	0	0	0	0	1- ϕ
M2	0	0	0	0	ψ	0	0	0	0	0	0	0	1- ψ	0	0	0	1- ϕ
m2	0	0	0	0	0	ψ	0	0	0	0	0	0	0	1- ψ	0	0	1- ϕ
F2	0	0	0	0	0	0	ψ	0	0	0	0	0	0	0	1- ψ	0	1- ϕ
f2	0	0	0	0	0	0	0	ψ	0	0	0	0	0	0	0	1- ψ	1- ϕ
†	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

iii) 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
TdF2	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

iv) matrix P

$$\begin{matrix}
& OM1 & Om1 & OF1 & Of1 & OM2 & Om2 & OF2 & Of2 & cM1 & cm1 & cF1 & cf1 & cM2 & cm2 & cF2 & cf2 & \dagger \\
M1 & 1-p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
m1 & 0 & 1-p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & p & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
F1 & 0 & 0 & 1-p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & p & 0 & 0 & 0 & 0 & 0 & 0 \\
f1 & 0 & 0 & 0 & 1-p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & p & 0 & 0 & 0 & 0 & 0 \\
M2 & 0 & 0 & 0 & 0 & 1-p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & p & 0 & 0 & 0 & 0 \\
m2 & 0 & 0 & 0 & 0 & 0 & 1-p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & p & 0 & 0 & 0 \\
F2 & 0 & 0 & 0 & 0 & 0 & 0 & 1-p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & p & 0 & 0 \\
f2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & p & 0 \\
\dagger & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1
\end{matrix}$$

v) matrix S

$$\begin{matrix}
& 0 & 1 & 2 & 3 & 4 & 5 & 6 \\
OM1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
Om1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
OF1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
Of1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
OM2 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
Om2 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
OF2 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
Of2 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
cM1 & 0 & s & 0 & 1-s & 0 & 0 & 0 \\
cm1 & 0 & s & 0 & 1-s & 0 & 0 & 0 \\
cF1 & 0 & 0 & s & 1-s & 0 & 0 & 0 \\
cf1 & 0 & 0 & s & 1-s & 0 & 0 & 0 \\
cM2 & 0 & 0 & 0 & 0 & s & 0 & 1-s \\
cm2 & 0 & 0 & 0 & 0 & s & 0 & 1-s \\
cF2 & 0 & 0 & 0 & 0 & 0 & s & 1-s \\
cf2 & 0 & 0 & 0 & 0 & 0 & s & 1-s \\
\dagger & 1 & 0 & 0 & 0 & 0 & 0 & 0
\end{matrix}$$

AIC was used to competitively rank models and infer biological scenarios. While maintaining an age effect on survival, primarily multiple combinations of the age-recapture probability relationship were explored. Subsequently, additive relationships with age, site, sex, time and capture heterogeneity were explored on all identified age classes. Afterwards, maintaining the best parametrization of recapture probabilities, the effects of sex and site on survival were explored. Lastly, different parametrizations of the age effect on survival probabilities, namely linear, logarithmic and quadratic versus discrete were investigated, as well as different ages at plateau. The results from the best-fit discrete model were superimposed against those aided by covariates and possible benefits and drawbacks were noted.

1.1.3.3 Population sizes and age-specific sex ratios

Population sizes and OSRs with 95% confidence intervals (CIs) were obtained using parametric bootstrapping (10,000 bootstraps) based on the variance-covariance matrices of model estimates and implemented in R v0.99.879 (R Core Team 2014) using the packages 'MASS' (Venables & Ripley, 2003), 'boot' (Canty & Ripley, 2012) and 'popbio' (Stubben & Milligan, 2007). Precisely, raw numbers of captured adult females and males of both localities were divided by their respective capture probabilities. Due to sex uncertainty at first capture and age-specificity, populations sizes of neonate-to-nine-year-olds were estimated using an additional variable - initial state probabilities of being a given sex multiplied by the raw numbers of captured individuals, averaged between years of capture, which were then divided by the respective capture probabilities. Finally, age-specific OSRs were calculated ($N[\♂]/N[\♀]$).

1.1.3.4 Survival temporal variance & canalization

Gould & Nichols (1998) introduced a method for the estimation of the true temporal variance of a given trait by removing the sampling variance from the total variance. This approach was used to calculate the standard deviations of mean sex-specific annual adult survival in Hermann's tortoises from Golem Grad Island. A sex-specific time dependent survival model was used to extract annual

survival probabilities and their respective variance-covariance matrices. Due to a lack of replicate populations, and in order to provide uncertainty measures to variance estimates, the original CR-histories were bootstrapped and mean annual survival temporal variances extracted for each bootstrap. Since E-SURGE does not offer this option automatically, the sample was limited to 50 manually obtained bootstraps. The variance of variances was subsequently obtained, providing CIs.

1.1.3.5 Population projections

Estimated demographic parameters from the best-fitted models of adult and early-life age-specific survival (see results) of Hermann's tortoises on Golem Grad Island were integrated in a deterministic pre-breeding population matrix model with 10 age classes and both sexes (Caswell 2001). Since our results implied a survival plateau at five years of age and no sex-specificity, five- to nine-year olds received the at-plateau survival estimate, no estimates differing between the sexes up to nine years of age; 10-year-olds received the respective adult sex-specific values. In another run, we applied an even worse case scenario where female tortoises received lower survival values from the age of eight, since our results implied that on Golem Grad females likely become a target to male sexual coercion around that age and females from the Island Plateau do indeed express lower survival values (see results). In the attempt to evaluate whether adult survival could explain present Golem Grad OSR, initial OSR was considered to be one, fecundity we set to the average value provided for the species (4.3) and reproduction was allowed from the age of eight (Bertolero et al. 2011). Additionally, in order to see the effect of sex differences in survival on annual population growth rate, we performed the same analyses without sex-specific survival (using the male estimates).

(SSB, individual observed in an active homosexual behaviour, essentially a male mounting another male, thus excluding combats), and dead (*f*).

TABLE 6A. Behaviours (resightings of 1,737 individuals, 2008–2014) were classified into 3 main categories: inactive, active, or sexual; (A) and (P) mean, respectively, sexually active versus sexually passive. Sample size (N) indicates the total number of observations; for example, 15 pairs of fighting males involve 30 individuals (some information was missing). SSB (%) indicates the actual number and proportion of SSBs observed; these involved only males (except for one female mounting another female).

Behaviour	Definition	Category	N	SSB (%)
Burrowed	Partly burrowed, head and legs retracted	Inactive	677	
In the shade	Motionless in the shade	Inactive	2513	
Basking	Fully exposed to sunrays, legs deployed	Active	1729	
Foraging	Eating plant, fungi, or animals	Active	195	
Hiding	In shelter (bush, undergrowth, etc.)	Active	718	
Walking	Walking alone	Active	755	
Chased	Trying to escape from a sexual assault of a male	Sexual (P)	30	25 (83)
Chasing	Male pursuing a conspecific	Sexual (A)	31	25 (81)
Courted	Courted by a mail	Sexual (P)	22	10 (45)
Courting	Male courting a conspecific, mounting attempts	Sexual (A)	22	10 (45)
Fighting	Male to male combat, violent shell shocks, and bites	Sexual (A)	30	0 (0)
Sex group	Sexually active group, e.g. 2-5males courting a female	Sexual	101	36 (36)
Mounting	Male mounting any conspecific, vocalizing, ejaculation	Sexual (A)	667	506 (76)
Necrophilia	Male mounting a dead tortoise, vocalizing	Sexual (A)	5	5 (100)
Skeletophilia	Male mounting an empty carapace, vocalizing	Sexual (A)	5	5 (100)
Sex train	Several males forming a line while pursuing a female	Sexual	3	0 (0)
Not classified	Missing information, ambiguous behavior, dead individual		2075	

All states can then transition via the survival matrix Φ (Table 7A), and given that they survive they can either stay in their state or transit into an either passive or sexually active (homosexual or heterosexual) state via matrix Ψ (Table 7A). Detection probability was modelled according to sexual behaviour in matrix P (Table 7A).

TABLE 7A. Elementary matrices: Survival matrix Φ , s is the probability that each behavioural state will survive from t to $t+1$; sexual activity transition matrix Ψ , ψ is the probability to transit between sexual behaviour states i.e. from sexually passive to a heterosexually active individual (SP-HSB), from sexually passive to a same-sex sexually active individual (SP-SSB), from heterosexually active to same-sex sexually active and *vice versa* (HSB-SSB and SSB-HSB, respectively), or from any sexually active state to a sexually passive one (HSB-SP and SSB-SP); detection probability matrix P , p is the probability of being observed as sexually passive (p^{SP}), heterosexually active (p^{HSB}), or same-sex sexually active (p^{SSB}).

matrix Φ					matrix P				
	SP	HSB	SSB	t		NO	SP	HSB	SSB
SP	s^{SP}	0	0	$1 - s^{SP}$	SP	$1 - p^{SP}$	p^{SP}	0	0
HSB	0	s^{HSB}	0	$1 - s^{HSB}$	HSB	$1 - p^{HSB}$	0	p^{HSB}	0
SSB	0	0	s^{SSB}	$1 - s^{SSB}$	SSB	$1 - p^{SSB}$	0	0	p^{SSB}
t	0	0	0	1	t	1	0	0	0

matrix Ψ				
	SP	HSB	SSB	t
SP	$1 - (\psi^{SP-HSB} + \psi^{SP-SSB})$	ψ^{SP-HSB}	ψ^{SP-SSB}	0
HSB	ψ^{HSB-SP}	$1 - (\psi^{SP-HSB} + \psi^{HSB-SSB})$	$\psi^{HSB-SSB}$	0
SSB	ψ^{SSB-SP}	$\psi^{SSB-HSB}$	$1 - (\psi^{SSB-SP} + \psi^{HSB-SSB})$	0
t	0	0	0	1

Survival (Φ) was constrained to be constant over time and state but was allowed to vary with sex and site. Transitions between sexual behaviours (Ψ) were held constant over time but they were sex, site, and state dependent. Detection probability (P) was time, sex, site, and state dependent to allow us to take into account variations in detectability. Our initial model was thus $\Phi(\text{sex} \times \text{site}) \Psi(\text{sex} \times \text{site} \times \text{state}) P(\text{sex} \times \text{site} \times \text{state} \times t)$. We then built alternative models to test specific hypotheses by using a backwards stepwise procedure while removing effects from each parameter in order to obtain the best linear combination at each step. Model selection was first performed on detection probability by testing time, sex, site, and state dependencies. We then tested for sex and site

dependencies for survival. Finally, we tested for site dependency on transition probabilities between behavioural states, thus testing for an effect of OSR and density.

1.1.4.2 Sexual coercion (index of cloacal damage)

Data were collected from mature and presumably immature ($82 < \text{SCL} < 150$) females from both localities. Only small individuals that could be sexed were retained. Field surveys were performed in May, June and July 2016 and 2017. A photo of the cloacal region of each female was taken by gently pulling the tip of the tail (Fig. 1A). Possible wounds in the supracaudal area were not clearly visible from photographs and were not included in the analyses. Some females were captured and photographed two or three times. The Golem Grad sample included 69 individuals and 101 pictures (May N=51, June N=27, and July N=23) whereas 139 individuals and 158 pictures were collected in Konjsko (May N=22, June N=111, and July N=25).

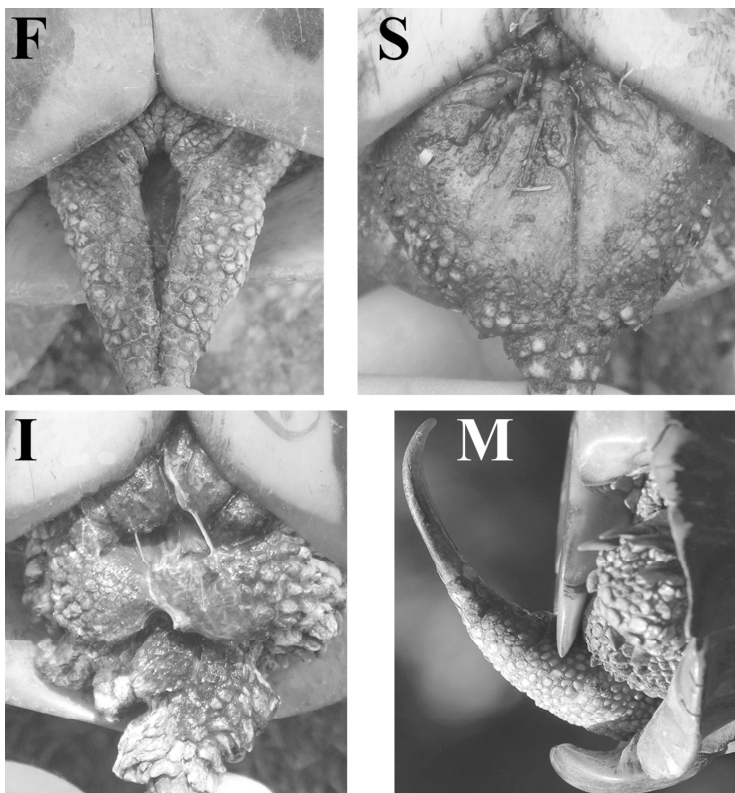


FIGURE 1A. Photographs of female's cloacal regions categorised for swollenness (S) from 0 to 3, and injury level (I) from 0 to 2. Female's normal cloaca (F) and male's horny tail (M, Photographed by X.B.). Figures S and I represent highest levels of swollenness and injury, respectively.

Pictures were visually scored for cloacal swollenness (0: not swollen, 1: slightly swollen, 2: clearly swollen, 3: extremely swollen, Fig. 1A) and for injury severity (0: no injury, 1: several injuries, 2: severely injured, Fig. 1A). Since the cloaca is soft and exhibits a relatively labile shape, it is not measurable by classical morphometric methods, thus we used visual ranking (Hailey 1990). To minimise the subjective nature of this method, photographs were randomly sorted into 15 sheets with 10 to 25 pictures in each. They were blindly categorised by two observers independently. In most cases, both scores were in agreement (swollenness: 49% total agreement, 44% slight disagreement, 7% partial disagreement, 0% full disagreement; injury levels: 64% total agreement, 35% partial disagreement, 1% full disagreement). Importantly, the overall proportions provided by each observer were either very close considering cloacal injuries or provided relatively similar trends for swollenness (Table 1). For most analyses we used average values from the double scoring. This generated seven levels of swollenness (0, 0.5, 1... 3) and five levels of injury severity. For conciseness, we also performed several analyses with a reduced level of scores. For example, using only three injury levels: 0 (0 - 0.5 pooled), 1 (1.0), and 2 (1.5-2.0 pooled).

Our sample included 208 individuals and 259 pictures (i.e. 51 pseudo-replicates). Females sampled more than once were captured at different months or different years. Consequently, a substantial amount of time elapsed between captures and their status changed (improving or worsening) in 79% of the cases. Consequently, re-sampling several individuals did not change the results significantly (analyses were nonetheless performed using all pictures, N=259, versus after random selection of pseudo-replicates, N=208).

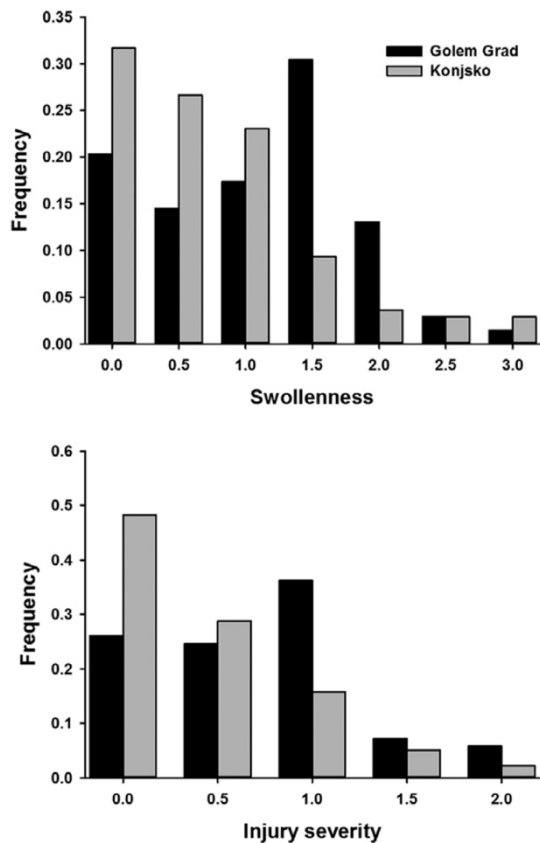


FIGURE 2A. Comparison of the prevalence (frequency, y-axis) of sexual harassments between the two neighbouring tortoise populations. Two proxies of coercive mating in females were used (x-axes): levels of cloacal swollenness (upper panel) and levels of cloacal injuries (lower panel). See text for details and statistics.

In practice, swollenness and injury levels provided similar trends (Fig. 2A). Indeed, the average values of swollenness positively correlated with injury scores (Spearman rank correlation $R_s=0.39$, $N=259$, $p<0.05$ [$R_s=0.41$ discarding pseudo-replicates]), simply because injuries entail tissue inflammation. Yet, injury scores likely better reflect the intensity of damages caused by males. For conciseness we emphasized injury levels results. Several continuous variables were not normally distributed (e.g. SCL); Box-Cox transformations were used. The resulting Henry's probability plots revealed linear patterns

1.1.5 LOCOMOTOR PERFORMANCE, HABITAT TYPE & SEXUAL COERCION

1.1.5.1 Steep cliffs, carapaces & swift escapes

Noticeable shell damage (breaks, cracks, blood, etc., Fig. 17) are always carefully described. Records were matched against locality change (e.g. Island Plateau to Beach), broken shells very likely implying a previous fall from the cliffs; at four occasions falling tortoises were directly observed in the field

(Golubović, Arsovski, Ajtić, Tomović, & Bonnet, 2013). The proportion of females vs. males that have died after taking the plunge (i.e. broken shell) *vis-à-vis* the total number of dead recoveries were compared using a chi-2 test with Yates correction for small samples.

1.1.5.2 Locomotor performance under sexual coercion

Thirteen adult female tortoises from Golem Grad (8) and Konjsko (5) were subjected to a behavioural experiment - an enclosure setup procedure testing their willingness to choose a risky exit under varying intensity of sexual coercion. A 2m² (2 × 1 m) rectangular enclosure with an opening (large enough to comfortably fit a fully-grown adult Hermann's tortoise) on one of the shorter sides was constructed (Fig. 3A). It faced an abrupt fall under which the ground was lined with Styrofoam covered with substrate and leaves to break the fall. Females that took part in the test were placed in the enclosure twice, thirty minutes each. First, each female was placed among five sexually charged Golem Grad males (a common Island occurrence, 3.4). Second time around, females



FIGURE 3A. Tortoise test enclosure (brightened) on Golem Grad island with opening facing abrupt fall.

were placed in the enclosure alone. The order of tests was deliberate in order to make sure that a jump in the presence of males was not promoted by previous knowledge, whereas not taking the exit when alone implied complete reluctance to jump. During both tests, the times the edge of the enclosure was approached by a female was noted. Importantly, whether a female jumped intentionally, or was pushed by a male

(example videos of both scenarios in Appendix) was noted. Primarily, the proportions of females from both localities that took the plunge vs. those that stayed in the enclosure for 30 minutes were tested in both scenarios (alone and with five males). Finally, the times the edge of the enclosure was approached in both scenarios was compared between localities. All comparisons were tested using a chi2 with Yates correction for small samples in R v0.99.879 (R Core Team 2014).

1.1.6 PHYSIOLOGICAL FRAMEWORK

Blood samples (100–300 μ L, adjusted to tortoise body size) were taken during activity time (morning and afternoon) from the jugular vein or cervical sinus using very small needles (27–30 G) and slightly heparinized 1-mL syringes. Blood was centrifuged in the field, plasma samples were immediately stored in liquid nitrogen, and then at -25°C in the laboratory until assays. Plasma T levels were measured by radioimmunoassay at the CEBC (Lagarde et al. 2003) on 50 μ L of plasma after diethyl ether extraction (efficiency 0.93 ± 0.1 , standard deviation [SD]). Cross-reactivity of the specific antibody (Sigma Laboratory) with other steroids was low (B/B0: 5α -dihydrotestosterone: 17.8%; 5β -androstene- 3β , 17β -diol: 1.4%; 5α -androstene- 3β , 17β -diol: 1.2%; androstenedione: 1.4%; epitestosterone: 0.7%; progesterone: 0.07%). The assay's sensitivity was 7.8 pg by tube, that is, 156 pg/mL. Intra-assay and interassay variations were 6% and 12%, respectively.

1.1.6.1 Sexual behaviours

In order for precise behaviour to be assigned to testosterone (T) levels, blood samples were rapidly taken (less than three minutes on average, range 0.2–7 minutes) on a random subset of the adults monitored in 9.1.3.1. In the field it was ensured that individuals did not detect the observers (i.e. no sign of disturbance) at capture. This fast procedure limited the possible rapid negative effect of stress on steroid levels (Michel & Bonnet, 2014), thus T levels and behaviours were considered to have been recorded simultaneously. Using the same method blood samples were collected from Konjsko as well. In total, 283

blood samples were collected (N=216 on Golem Grad [31 females and 185 males] and N=67 on Konjsko [46 females and 12 males]).

1.1.6.2 Male maturity

A random sample of 492 Hermann's tortoises (94 females, 379 males and 19 unsexed) was collected paying attention that the broadest possible body size spectrum was represented. It was particularly important that the range of body sizes when maturity supposedly happens (130-150mm, Bertolero et al. 2011) is sampled. Plasma T levels were plotted against SCL.

1.1.7 ADDITIONAL GOLEM GRAD ISLAND INFO

Finally, here I present screenshots of four information boards produced as part of a Rufford Nature Conservation Grant (20915-1), that now welcome visitors to the island:

фреска од црквата Св. Петар прикажувајќи ги "Опасата на Цариград" и "Бегството од Египет"

St. Peter church fresco depicting "The Siege of Tsarigrad (Constantinople)" and "Escape from Egypt"

Накит, V/VI век
Jewelry, V/VI century

Накит, IV век
Jewelry, IV century

Островот Голем Град е единствениот остров во Македонија кој на 2km од брегот на Пречна Планина (дел од планината Галичица) се издигнува од големото Преспанско Езеро (842m надморска висина). Неговата површина изнесува ~20 хектари (~680m должина север-југ и ~430m ширина исток-запад) со највисока точка од 901m надморска висина. Климата е изменето континентална до субмедитеранска. Густо населениот и разновиден животен свет, заедно со изобилните од археолошки ископини, на ова мало парче земја целосно му го заслужиле статусот на строго заштитена зона во рамките на Националниот Парк "Галичица".

The island of Golem Grad is the only island in the Republic of Macedonia. Situated 2km off the coast of Mt. Prechna (part of Mt. Galichica) in the large Prespa Lake (842m asl) it covers a surface area of ~20 hectares (~680m long north-south and ~430m wide east-west) summing at 901m asl. The climate is mild continental to submediterranean. Dense and diverse animal and plant populations along with abundant archeological findings have rightfully so bestowed to the island the status of a strictly protected area within National Park "Galichica".

Погребувањата од античкиот период на Голем Град сведочат за човечки живеалишта кои датираат од IV – I век п.н.е. и од IV – VI век од новата ера. Најраните познати населеници му припаѓале на племето Орести, додека пак најраните откриени куќи се од хеленистичкиот период во околината на црквата Св. Димитрија (види мапа). Од римската епоха се откриени неколку куќи на кои им служела и цистерна (види мапа) сместена во нивната непосредна близина.

Graves and uncovered grave goods on Golem Grad testify to island settlements in antiquity dating back from the IV – I century BCE, as well as from the IV – VI century CE. The earliest known inhabitants belonged to the tribe Oresti. During the Hellenistic period there were houses around the area of St. Demetrius church (see map), whereas from the Roman period few houses have been uncovered near what used to be a Roman cistern (see map).

Pelecanus crispus

Во средниот век островот претставувал манастирски комплекс каде биле изградени повеќе цркви (Св. Петар, Св. Димитрија, Св. Никола Влаја). Во манастирскиот комплекс биле погребувани монасите, но и верниците од околните населби на крајбрежјето кои биле духовно врзани со светците на островот. Погребувања на островот имало до XI век, а монашкиот живот се обновувал и до средината на XX век.

Глава на девојче, II век п.н.е.
Head of a girl, II century BCE

A monastery complex with several churches (St. Peter, St. Demetrius, St. Nikola Vlajja) was built during the Middle Ages. Monks found their final resting places in this complex, but also local people from the mainland villages that believed to be spiritually connected to the saints worshiped in the island's churches. Burials took place on the island until the XI century CE, but monks have been known to take up residence as late as the XX century.

Oryctolagus cuniculus

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ОСТРОВ

ГОЛЕМ ГРАД

GOLEM GRAD

ISLAND



Пристаниште "Годарица"
Dock "Gojdarica"

← Албанија
Albania

Грција
Greece →



Тука си!
You are here!

Пристаниште "Св. Петар"
Dock "St. Peter"

црква Св. Петар - XIV век
Ранохристијанска базилика - V - VI век
church of St. Peter - XIV century
Early Christian basilica - V - VI century

црква Св. Димитрија - XIV век
Хеленистичка куќа - II век п.н.е.
St. Demetrius church - XIV century
Hellenistic house - II century B.C.E.

Римска куќа
Roman house

Ранохристијанска базилика - V век
Early Christian basilica - V century

Ранохристијанска базилика - V - VI век
Early Christian basilica - V - VI century

Римска куќа - IV век
Roman house - IV century

Римска куќа
Roman house

Римска куќа - IV век
Roman house - IV century

Римска цистерна - IV век
Црква - XIII - XIV век
Roman cistern - IV century
Church - XIII - XIV century

Црква - XIV век
Church - XIV century

Пристаниште "Влаија"
Dock "Vlajja"



Маркантната шума од фоја (*Juniperus excelsa*) целосно го покрива платото создавајќи услови за живот за скоро сите останати живи форми на Голем Град. Покрај сенките кои ги создава, шумата претставува и основна инфраструктура за гнездење на голем број видови птици, меѓу кои и стотиците корморани (*Phalacrocorax carbo*) чиј измет го дава белиот изглед на нивните фои домаќини.

The juniper (*Juniperus excelsa*) forest on the island fully covers the plateau, creating habitats for almost all Golem Grad life forms. Besides providing shade, the forest creates a nesting infrastructure for many bird species. Many trees are of white colour due to the huge amounts of guano deposited on them regularly by the hundreds of nesting great cormorants (*Phalacrocorax carbo*).

Под платото, илјадници обични и кадроглави пеликани (*Pelecanus onocrotalus* и *P. crispus*) одмараат од риболов небаре совршено камуфлирани среде белите камени плажи. Островот го имаат направено свој дом и некои грабливи птици, меѓу кои и големиот ушест був (*Bubo bubo*) со распон на крилја до 188cm. Тој се гнезди во стрните карпи од островот, кои истовремено нудат засолниште и за густите популации од големата пштарка (*Apus melba*). На изгрејсонце и зајдисонце пејзажите од околното езеро и планини се накинети од стотици пштарки во игра и лов. **Импозантните популации на птици кои се гнездат овде, ловат, или го користат островот како привремено засолниште се резултат на непостојаното присуство на човекот, како и изолираноста на островот, а со тоа и отсуството на непознати предатори (мачки, стаорци, итн.). Нека остане така!**

Under the plateau, Golem Grad's beaches host thousands of great white and Dalmatian pelicans (*Pelecanus onocrotalus* and *P. crispus*) camouflaged almost perfectly against the surrounding white cliffs and rocks during fishing breaks. Birds of prey also inhabit the island, the largest of which is the Eurasian eagle-owl (*Bubo bubo*) with a wingspan of up to 188cm. It nests on the steep cliffs surrounding the plateau, also used by the dense population of alpine swifts (*Apus melba*). At dusk and dawn the lake and mountain landscapes around the island are flooded by hundreds of parading and hunting swifts. **The impressive bird populations that nest, hunt, or use the island as a stopping ground, are a consequence of the infrequent human presence and lack of alien predators (cats, rats, etc.) due to the isolation of the island. Let's keep it that way!**

Птиците се најгласните а со тоа и највпечатливите жители на островот, меѓутоа далеку од единствени. Тука се исто така присутни и габи (*Battarrea phalloides*, *Geastrum fornicatum* итн.) како и без'рбетници, меѓу кои, пеперутки (*Aglais io*, *Limenitis reducta* итн.), твдокрилки (*Cyphogenia lucifuga*, *Zabrus incrassatus* итн.), стогоналки (*Scolopendra cingulata*), итн. Островот е и дом на влекачи (погледнете ја соседната табла) како и цицачи - видра (*Lutra lutra*) и лилјаци (*Miniopterus schreibersii*, *Rhinolophus ferrumequinum*, и риболовецот *Myotis capaccinii*). Низ островот може да се видат и црни, жолти и бели зајци дупкари (*Oryctolagus cuniculus*), кои биле донесени на почетокот од минатиот век. Покрај зајците, кога бил населен островот, човекот донел и култивирал повеќе видови на корисни растенија кои сеуште се присутни во подивена форма. Винова лоза (*Vitis vinifera*), дубовник (*Citrullus lanatus*) и смоква (*Ficus carica*).

Birds are the loudest and most conspicuous inhabitants of Golem Grad, but surely not the only ones. You can also find fungi (*Battarrea phalloides*, *Geastrum fornicatum* etc.), as well as invertebrates, such as butterflies (*Aglais io*, *Limenitis reducta* etc.), beetles (*Cyphogenia lucifuga*, *Zabrus incrassatus* etc.), centipedes (*Scolopendra cingulata*), etc. The island is also home to reptiles (see the next board), as well as mammals – the otter (*Lutra lutra*) and bats (*Miniopterus schreibersii*, *Rhinolophus ferrumequinum* and the fishing *Myotis capaccinii*). Around the island, you can also see black, orange and white rabbits (*Oryctolagus cuniculus*), that have been brought here at the beginning of the previous century. Besides rabbits, throughout the ages the island was inhabited, man had brought and cultivated several plant species that have now become naturalized: grape wine (*Vitis vinifera*), watermelon (*Citrullus lanatus*) and fig (*Ficus carica*).

Фотографии и илустрации од/Photographs & illustrations by:
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Во 2008 година истражувачи од Македонското Еколошко Друштво, Факултетот по биологија при Универзитетот во Белград, Србија и од Центарот за биолошки истражувања во Шизе, Франција започнаа долгорочни популациони студии на три од четирите видови влекачи на островот Голем Град: рибарката (*Natrix tessellata*), поскокот (*Vipera ammodytes*) и Херманиевата желка (*Testudo hermanni*). Досега (2018) се обележани преку 1800 желки, 500 поскоци и преку 7000 рибарки за кое време се забележани бројни особености. Прочитајте повеќе за:

In 2008, researchers from the Macedonian Ecological Society, the Faculty of Biology at the University of Belgrade, and from the Centre for Biological Studies of Chizé, France initiated long-term population studies on three of the four reptile species on the island: the dice-snake (*Natrix tessellata*), the horn-nosed viper (*Vipera ammodytes*) and the Hermann's tortoise (*Testudo hermanni*). Until now (2018), over 1800 tortoises have been marked, 500 vipers and over 7000 dice-snakes, during which many peculiarities have been uncovered and studied: Read more in:

- Заканите за рибарките – “*Natrix tessellata* on Golem Grad, Macedonia: a natural fortress shelters a prosperous snake population” by Sterijovski et al. [2011, *Mertensiella* **18**: 298-301]
- Агилните желки на островот – “Moving in the real world: tortoises take the plunge to cross steep steps” by Golubović et al. [2013, *Biological Journal of the Linnaean Society* **108**: 719-726]
- Импресивната популација на рибарки – “Unexpected life history traits in a very dense population of dice snakes” by Ajtić et al. [2013, *Zoologischer Anzeiger* **252**: 350–358]
- Поскокот со голем апетит и тажна судбина – “Two fangs good, a hundred legs better: juvenile viper devoured by an adult centipede it had ingested” by Arsovski et al. [2014, *Ecologica Montenegrina* **1**: 6-8]
- Густата популација на желки со нерамножен однос на полови и хомосексуално однесување – “The prison effect in a wild population: A scarcity of females induces homosexual behaviors in males” by Bonnet et al. [2016, *Behavioral Ecology* **27**: 1206–1215]
- Шемите на раст на островските желки - “When carapace governs size: variation among age classes and individuals in a free-ranging ectotherm with delayed maturity” by Arsovski et al. [2018, *Oecologia* **186**: 953:963]
- Агресивните сексуални игри на желките - “Is sexual brutality maladaptive under high population density?” by Golubović et al. [2018, *Biological Journal of the Linnaean Society* in press]

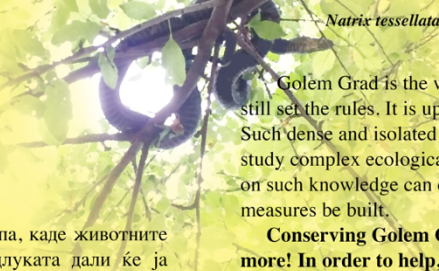


Голем Град е дивниот бисер на Преспа, каде животните сеуште владееат. Во нашите раце е одлуката дали ќе ја оставиме природата да продолжи да го крои патот на овој остров. Оваа густа и изолирани популации се едни од ретките сочувани примери во природата кои нудат можност да се проучуваат еколошки и еволутивни процеси од малтене секаков размер. Само со вакви познавања може да се скројат ефективни и ефикасни конзервативски решенија.

Сочувувањето на Голем Град би значело сочувување на многу повеќе! За да помогнете, во најмала рака, останете на туристичката патека, не ги вознемирувајте животните и почитувајте ги како ваши домаќини. Малите желчиња се некогаш неодоливи, меѓутоа во вакви специфични популации не заборавајте дека отсуство на токму една единка би можела да направи разлика помеѓу пропаст и напредок.

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Golem Grad is the wild jewel of Prespa, where animals still set the rules. It is up to us whether this will stay the case. Such dense and isolated populations offer a rare opportunity to study complex ecological and evolutionary phenomena. Only on such knowledge can effective and efficient conservation measures be built.

Conserving Golem Grad would mean to conserve much more! In order to help, in the very least please stay on the tourist paths, and act as a guest on this wild island whose inhabitants do not wish to be disturbed. Small tortoises can look tempting to take, but in peculiar populations like this one, the absence of even one individual could make the difference between disaster and progress.

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Vipera ammodytes



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