REPORT

Life history traits of the sea snake *Emydocephalus annulatus*, based on a 17-yr study

Richard Shine[1,2] · Terri G. Shine[1] · Gregory P. Brown[1] · Claire Goiran[3]

Abstract Although sea snakes are important predators in coral reef ecosystems and have undergone substantial population declines in some areas, we have little robust information on life histories of these animals. Based on a 17-yr mark–recapture study of turtle-headed sea snakes (*Emydocephalus annulatus*) in New Caledonia (> 1200 individuals marked), we can confidently allocate ages to 539 individuals (1–11 yr of age). Using data for those snakes, we describe patterns of growth and reproduction. Using the entire data set, we also estimate annual rates of survival. One to three large offspring (300 mm snout–vent length [SVL]) are born after a prolonged (8-month) gestation. The young snakes grow rapidly until they are about 2 yr old (500 mm SVL), after which growth slows, especially in males. Most females begin reproducing at 3 yr of age, and they produce a litter (typically of two offspring) in about 2 out of every 3 or 4 yr thereafter. Annual survival rates are around 70%, but some individuals live for more than a decade. Overall, the life history of this species involves rapid growth and early maturation, followed by low but sustained reproductive output. Despite their relatively recent evolutionary origin, hydrophiine sea snakes are remarkably diverse in life histories as well as in

morphologies and diets. Hence, even closely related taxa may differ substantially in their vulnerability to threatening processes.

Introduction

Diverse and abundant in coral reefs of the IndoPacific, sea snakes play important ecological roles as mesopredators (Reed et al. 2002; Ineich et al. 2007). Thus, rapid declines of populations of sea snakes have raised widespread concern about the conservation status of this group and the trophic consequences of their extirpation (Udyawer et al. 2018). Puzzlingly, some of those declines have occurred in areas protected from overt anthropogenic impacts (e.g. Goiran and Shine 2013; Lukoschek et al. 2013). The uncertain causation for population decline suggests that we urgently need to understand more about the life histories of sea snakes. For example, traits such as slow growth, delayed maturation and infrequent reproduction can render a population more vulnerable to threatening processes (e.g. Reed and Shine 2002; Webb et al. 2002). Unfortunately, robust information on this topic is rare for sea snakes, because of the logistical challenges involved (Udyawer et al. 2018).

Some life history traits (such as mean adult body sizes, mean litter sizes, proportion of adult females that are reproductive when sampled) can be determined from "snapshots"—for example, by dissecting snakes that are taken as bycatch by commercial trawlers (e.g. Ward 1996; but see Fry et al. 2001 for a discussion of possible biases due to non-random catchability). Much of what we know

✉ Richard Shine
rick.shine@mq.edu.au

1 Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia

2 School of Life and Environmental Sciences, University of Sydney, Sydney, NSW 2006, Australia

3 LabEx Corail and ISEA, Université de la Nouvelle-Calédonie, BP R4, 98851 Nouméa Cedex, New Caledonia

about the ecology (especially, diets) of sea snakes has been gathered in this way (e.g. Glodek and Voris 1982; Voris and Voris 1983). However, we cannot truly understand the life history (especially, traits such as age at maturation, longevity and frequency of reproduction) without knowing ages as well as sizes of the animals that we study. Such information can be obtained by examining growth zones in bones or otoliths, but the extensive validation studies required for this method are unlikely to be feasible in free-ranging sea snakes (e.g. Ward 2001).

The most reliable way to document age-related life history traits in a biological population is to conduct long-term mark–recapture studies, whereby the attributes and fates of known individuals can be tracked through time—preferably, for at least as long as mean longevity of individuals within the population (e.g. Tinkle et al. 1993). With most species of sea snakes, this would require prolonged time on boats, in remote areas, working with mobile and deadly animals. As a result, most long-term mark–recapture studies on marine snakes have been performed on amphibious species (laticaudine sea kraits and homalopsine mud snakes) where the investigators can gather data on land (e.g. Shine and Shetty 2001; Brischoux and Bonnet 2009; Chim and Diong 2013). To our knowledge, there have only been two published mark–recapture programs on fully aquatic (hydrophiine) sea snakes, and both have relied on relatively small sample sizes (43 recaptures more than a month apart in Burns and Heatwole's (2000) study of *Aipysurus laevis*; 38 recaptures more than 300 d apart in Masunaga and Ota's (2003) study of *Emydocephalus ijimae*). The authors of those studies used growth rates to estimate ages at maturation, because they did not know the ages of individual snakes (apart from young-of-the-year).

We have taken advantage of a logistically favourable study system to conduct a long-term (to date, 17 yr) mark–recapture study on turtle-headed sea snakes (*Emydocephalus annulatus*) in small bays beside the city of Noumea, in New Caledonia (e.g. see Shine et al. 2012; Goiran et al. 2013). First, the coral reef sites where this species lives are readily accessible from shore, eliminating the need for boats. Second, accommodation and laboratory facilities are available < 100 m from the study sites. Third, the water is clear and shallow, facilitating snorkelling rather than requiring scuba diving. Fourth, the snake species is harmless (unlike virtually all other hydrophiine species); the fangs and venom apparatus are greatly reduced due to the snakes' reliance on small fish eggs as their sole prey (e.g. Goiran et al. 2013). Fifth, these snakes are remarkably philopatric (Lukoschek and Shine 2012; Shine et al. 2012) and have small home ranges such that a marked snake is likely to be recaptured year after year throughout its life. Reflecting those advantages, we have accumulated data on more than 1200 snakes (total of >

2500 capture events) over the 17 yr of our study. The present analysis is based primarily on data from 539 snakes that we captured and marked in their first year of life, of which 271 were recaptured in subsequent years (up to 11 yr later). Thus, we can confidently assign ages to these recaptured individuals. That data set allows us to quantify life history traits in more detail than has been possible with most previous research on snakes.

Methods

Study species and area

The turtle-headed sea snake (*Emydocephalus annulatus*) is a relatively small (to 800 mm snout–vent length [SVL], in our study population) heavy-bodied hydrophiine elapid snake (Fig. 1). The species occurs in coral reef habitats in the Timor Sea and the Coral Sea (Nankivell et al. 2020) and feeds entirely on the eggs of small demersal-spawning blennies, gobies and damselfish (Goiran et al. 2013). Foraging snakes use chemical cues to locate nests (Shine et al. 2004) and often must overcome defence from nest-guarding fish (Goiran and Shine 2015, 2020). Male snakes > 500 mm SVL focus on mate-searching and courtship during winter months (Shine 2005a); female snakes > 500 mm SVL are gravid over the austral summer and produce offspring in May (see below).

Our studies were centred on two small shallow bays (Baie des Citrons [2 sites: north and south] and Anse Vata: 22° 16′ S, 166° 26′ E) beside the city of Noumea, in the Pacific archipelago of New Caledonia. Water depth ranges from 1 to 4 m at high tide, with an average tidal range of around 1.5 m (Goiran et al. 2020). The substrate consists of a mosaic of live coral, coral rubble and sand (Goiran et al. 2020). Detailed analyses have revealed few if any

Fig. 1 Turtle-headed sea snake (*Emydocephalus annulatus*). Photograph by C. Goiran

associations between an individual snake's phenotype (size, sex, colour morph) and the habitats with which it is associated (Shine et al. 2003; Goiran et al. 2020). Although our three study sites are separated by < 1.5 km, individuals rarely move between sites (Lukoschek and Shine 2012; Shine et al. 2012). For the present analyses, we combine data from all three sites in order to maximise sample sizes.

Methods for capturing and processing snakes

Every January from 2004 to 2020 (*n* = 17 yr), we have conducted mark–recapture surveys of these populations by snorkelling in shallow water during daylight hours. Each site is sampled about six times per annum, for 45–60 min per survey session. Teams consist of 2–14 people (but typically, around 4–6 people) who search for both active and inactive snakes. The animals are captured by hand and are retained in floating cages before being taken to a nearby laboratory to be measured (snout–vent length), weighed and (if not already carrying a tag) individually marked by insertion of a PIT tag on the posterior lateral surface. We classified snakes > 500 mm SVL as adults, based upon extensive data sets for males during the courtship season (i.e. males > 500 mm SVL exhibited courtship, whereas males below this size did not: e.g. Shine 2005a) and our palpations of females (i.e. almost all records of gravid snakes came from animals > 500 mm SVL). Adult males can be distinguished from females by a male's longer tail, more rugose skin and rostral spine (e.g. Avolio et al. 2006; Shine et al. 2012). PIT tags have been used for two of the populations (Anse Vata and Baie des Citrons south) from 2004, but tags have only been used in the third site (Baie des Citrons north) since 2016. Female snakes are palpated to detect and count oviductal embryos. The snakes are then released at their site of capture, usually < 90 min after they were first encountered. We clip a scale on the tail when a snake is processed and do not recapture these tail-marked snakes for the remainder of the trip. Thus, each snake is only captured and handled once per year, to minimise stress.

Statistical analyses

Examination of size-frequency distributions of the captured snakes revealed a distinctive cohort of small animals, undoubtedly young-of-the year (< 460 mm SVL: see Fig. 2). Birth occurs in May (see below), so these animals are in their first year of life (on average, 8 months old during the January census). We assigned an age of 1 yr to all animals within this size range. We then allocated an age class to those snakes when we captured them in subsequent years, giving us a total of 539 records for body sizes of known-age snakes, and 94 records for reproductive state and litter size in known-aged adult female snakes. To examine how these parameters shifted with age, we plotted body sizes, reproductive frequencies (proportions of gravid animals) and litter sizes against known ages.

We used ANOVA in JMP 13.0 to ask if the age-related variation in reproductive frequency and litter size was greater than expected under the null hypothesis. To estimate annual survival rate, we used the program MARK 8.2 (White and Burnham 1999) to estimate survival of sea snakes based on individual mark–recapture histories, including all snakes rather than only the known-age specimens. We fitted a full set of 16 Cormack–Jolly–Seber (CJS) models in which survival (phi) and recapture rates (*p*) were either held constant, varied between sexes, varied over time or varied over time in a different manner for each sex. We assessed the fits of the 16 CJS models by comparing their Akaike information criterion (AICc) values.

Results

Seasonal timing of gestation

Many of the adult females palpated in January contained large oviductal embryos. Based on dissection of occasional mortalities, we infer that ovulation occurs around September–October. Parturition occurs around May, based on the appearance of neonates in the population at this time (see below). Thus, gestation extends for around 8 months.

Sexual size dimorphism

Both sexes attain sexual maturity at around 500 mm SVL, but adult females grow larger than adult males (Fig. 2).

Offspring size

Neonates average around 300 mm SVL and 30 g in mass (*N* = 12 snakes captured 26 April to 30 May, mean SVL = 309.6 mm, SE = 0.47, range 290–335 mm; mean mass = 30.3 g, SE = 1.19, range 23–36 g).

Growth rate

Based on body lengths of known-age snakes, growth in length is rapid in both sexes until they are about 2 yr old (i.e. around 500 mm SVL). From that point on, growth is faster in females than in males. Older snakes continue to increase in size for at least 10 yr (Fig. 3).

Fig. 2 Frequency distributions of body size (snout–vent length) in turtle-headed sea snakes (*Emydocephalus annulatus*). **a** Body sizes of all snakes combined (*N* = 2406), **b** body sizes of adult females (*N* = 1005) and **c** body sizes of adult males (*N* = 945). The number on the *X*-axis represents the lower limit of each size category (e.g. "300" shows data for snakes between 300 and 320 mm SVL)
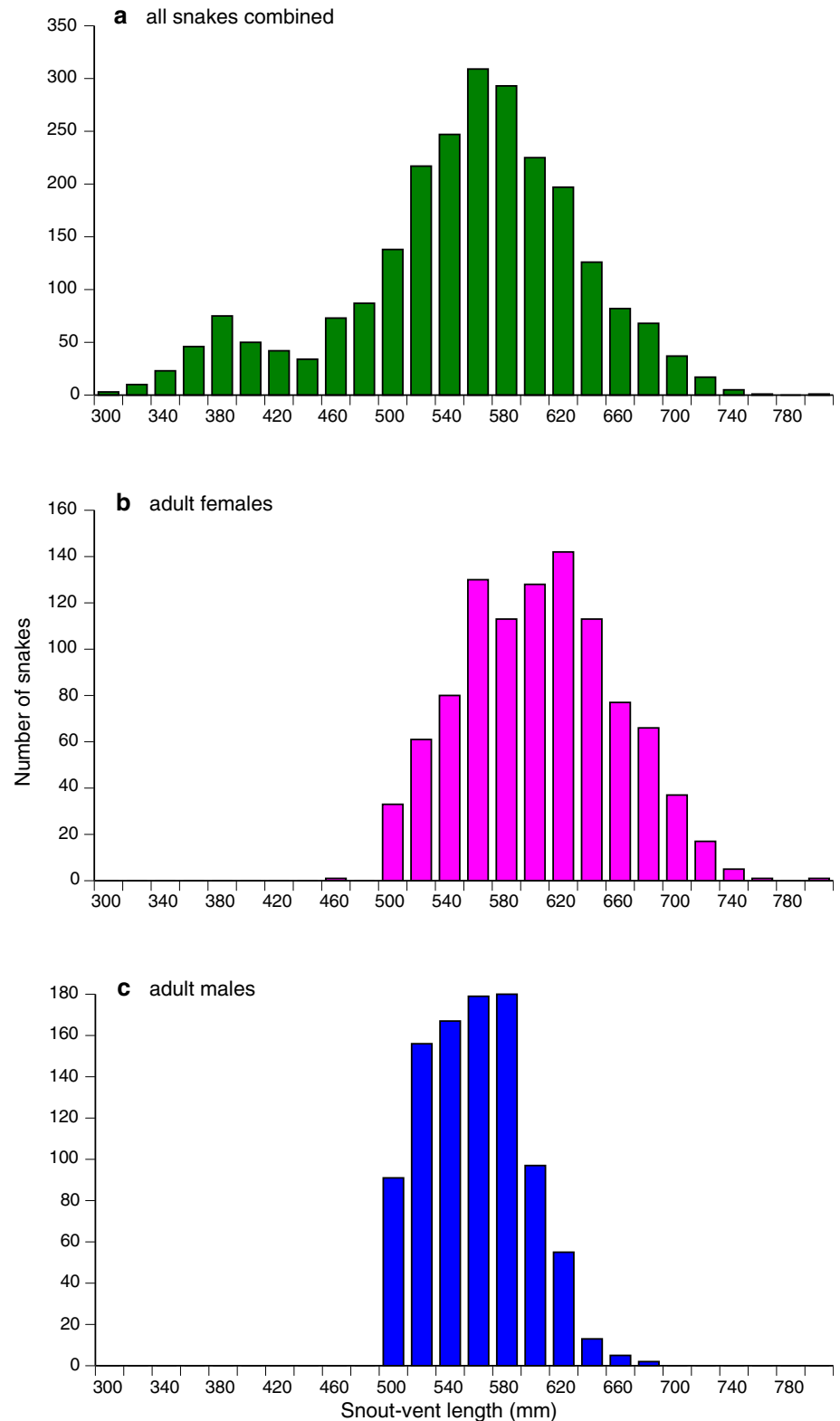
Reproductive frequency in females

Only one 2-yr-old female produced a litter (3% of the sample), but that proportion rose to at least 50% in all subsequent age classes (Fig. 3b). The proportion of adult females that were gravid in January averaged 68% (62 of 91 females that were at least 3 yr old when assessed). Excluding the single 2-yr-old animal that was gravid, the
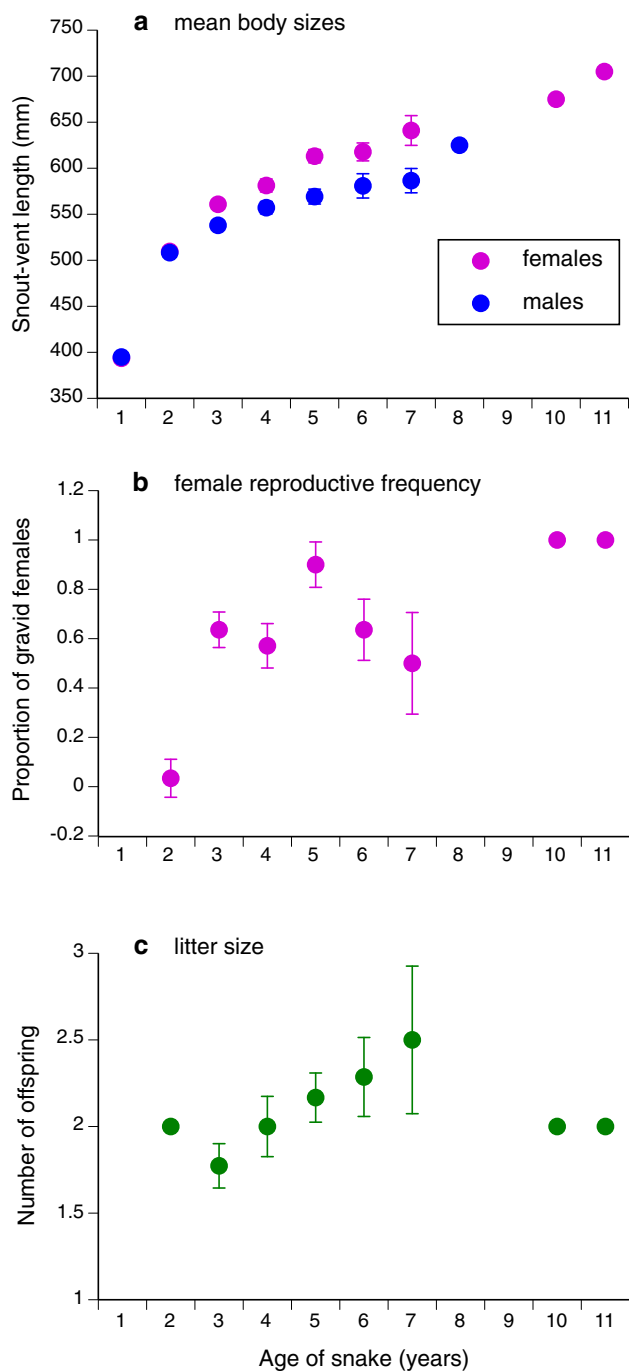
Fig. 3 Effects of age on **a** mean body size, **b** reproductive frequency in adult females and **c** mean litter size in known-age (individually marked) turtle-headed sea snakes (*Emydocephalus annulatus*). Vertical bars show standard errors

proportion of reproductive animals among adult females did not differ significantly among snakes of different ages ($F_{6,84} = 1.26$, $P = 0.28$). In the larger data set (including snakes for which ages were unknown), the proportion of adult-size females that were reproductive was 56.3% (564 of 1002 records).

Litter size

Palpation revealed a mean litter size of 2.01 (SE = 0.08, range = 1–3). The most common litter sizes were 2 ($N = 41$, = 64% of all records) followed by 3 ($N = 12$) and 1 ($N = 11$). Litter size did not change significantly with maternal age ($F_{7,56} = 1.06$, $P = 0.40$) but increased with increasing maternal SVL ($N = 64$, $r^2 = 0.12$, $P < 0.003$; Fig. 3c). In the larger data set (566 records), litter size averaged 2.06 (SE = 0.03, range 1–4).

Rate of annual survival

Table 1 ranks the fit of the top five CJS models. The best model was one in which both annual rate of survival and probability of recapture were allowed to vary among years. This model fit the data overwhelmingly better than any others (all $\Delta AICc > 6$). The next three best-fitting models also had the annual probability of survival modelled as time dependant (i.e. Phi(t)). The sexes exhibited similar annual rates of survival: the best model that incorporated separate estimates for males and females was #5 (based on $\Delta AICc$, this model was 21.98 × worse fit than the top model). Annual survival estimates from the top model ranged from 42 to 94% among years (Table 2), with a mean of 68.8% (SE = 3.3). Annual recapture probabilities ranged from 42 to 69% (Table 2), with a mean of 67.0% (SE = 2.1).

Discussion

At our study sites in New Caledonia, turtle-headed sea snakes exhibit seasonal patterns of reproduction and hence, of parturition. Neonates grow rapidly and typically attain sexual maturity at 2 yr of age (males) and 3 yr of age (females). Thereafter, an adult female produces litters (usually of two large offspring) in about 2 out of 3 yr. Females grow larger than males not because of higher survival rates, but because of higher rates of growth after maturation. Broadly, these traits (size at birth, gestation period, litter size, age at maturity, reproductive frequency, sexual size dimorphism) resemble those reported for a congeneric species from Japan (*E. ijimae*) (Masunaga and Ota 2003; Masunaga et al. 2003) but differ considerably from some other hydrophiine species. For example, Burns and Heatwole (2000) inferred a later age at maturation in *Aipysurus laevis* (4–5 yr in females) and high longevity (to > 15 yr). At the other extreme, some sea snakes mature early and have short lifespans (*Enhydrina schistosa* [*Hydrophis schistosus*] maturation 18 months, lifespan to 4 yr: Voris and Jayne 1979; *H. hardwickii* and *H. elegans* maturation 2 yr, lifespan 4–5 yr: Ward 2001).

Table 1 Rankings of the top five Cormack-Jolly-Seber models fit to mark–recapture data from turtle-headed sea snakes (*Emydocephalus annulatus*)

Model	AICc	ΔAICc	Likelihood	Parameters	Deviance
Phi(*t*) *p*(*t*)	4894.629	0	1	31	1184.257
Phi(*t*) *p*(.)	4901.203	6.5736	0.0374	17	1219.457
Phi(*t*) *p*(sex)	4902.657	8.028	0.0181	18	1218.879
Phi(*t*) *p*(sex*t*)	4912.89	18.2603	0.0001	47	1169.351
Phi(sex*t*) *p*(*t*)	4916.617	21.9881	0	47	1173.079

The models are ranked by corrected Akaike information criteria (AICc) weightings, with the best-supported model at the top of the table. Model parameters are annual survival (Phi) and recapture (*p*) rates. Different models have parameters constrained to be constant (.), varying among years (*t*), between sexes or varying among years in a different manner for each sex (sex*t*). In the best-fitting model (top), annual survival and recapture rates both vary among years

Table 2 Estimates of annual survival and recapture rates for turtle-headed sea snakes (*Emydocephalus annulatus*)

Year	Survival (± SE)	Recapture (± SE)
2004	0.65 (± 0.07)	0.58 (± 0.07)
2005	0.79 (± 0.07)	0.42 (± 0.05)
2006	0.77 (± 0.07)	0.53 (± 0.05)
2007	0.66 (± 0.05)	0.63 (± 0.05)
2008	0.84 (± 0.05)	0.65 (± 0.05)
2009	0.70 (± 0.07)	0.49 (± 0.06)
2010	0.42 (± 0.05)	0.69 (± 0.05)
2011	0.78 (± 0.06)	0.64 (± 0.06)
2012	0.62 (± 0.06)	0.45 (± 0.06)
2013	0.66 (± 0.06)	0.67 (± 0.06)
2014	0.94 (± 0.10)	0.46 (± 0.06)
2015	0.55 (± 0.07)	0.58 (± 0.07)
2016	0.66 (± 0.06)	0.55 (± 0.06)
2017	0.80 (± 0.08)	0.50 (± 0.06)
2018	0.50 (± 0.06)	0.64 (± 0.06)
2019	0.65 (± 20.67)	0.65 (± 20.66)

Estimates are produced from the top-ranked Cormack–Jolly–Seber mark–recapture model (see Table 1), for males and females combined

Mean offspring size in *E. annulatus* (300 mm SVL) is similar to that in *E. ijimae* (315 mm SVL: Masunaga et al. 2003), as is litter size (means of 2.74 in *E. ijimae*, 2.01 in *E. annulatus*). Using the metric of Lemen and Voris (1981), relative reproductive effort per embryo in *Emydocephalus* thus is among the highest reported for any hydrophiines (around 10.3% for *E. ijimae*). That result fits well with extensive data sets on the allometry of reproductive output in terrestrial snakes: relative to larger taxa, smaller species tend to produce fewer offspring, that are larger relative to maternal body size (Shine 2005b). Adult females of both *Emydocephalus* species are among the smallest sea snakes, and hence would be expected to produce small litters of large offspring.

Previous studies have pointed out that the adaptive radiation of hydrophiine sea snakes, although relatively recent, encompasses a substantial diversity in morphology (e.g. Sherratt et al. 2018) and ecology (notably, diets: Voris and Voris 1983; Heatwole 1999). The examples reviewed in the above paragraph suggest that the same is true of life histories. Selective forces imposed by the marine environment have favoured a constellation of traits rarely seen in terrestrial snakes (notably, the infrequent production of small litters of large offspring: Lemen and Voris 1981; Ward 2001) and a reduced overall investment into reproduction by females (Shine 1988). Despite those pressures for convergence, however, hydrophiine species vary considerably in traits such as ages at maturation, reproductive frequency and offspring sizes (see above) as well as relative clutch mass (Lemen and Voris 1981) and sexual size dimorphism (Shine 1994).

Our study is the first to report rates of survival in any sea snake population. The annual survival rate in our study population (70%) is similar to that of terrestrial snakes that mature at the same age as does *E. annulatus* (i.e. 3 yr; annual adult survival rates 62–80%, from a 1987 review by Parker and Plummer). More recent studies support this pattern: for example, average annual survival rates of adult snakes were estimated as 82% for the elapid *Hoplocephalus bungaroides* and 74% for the elapid *Cryptophis nigrescens* (Webb et al. 2002), around 70% for the viper *Vipera aspis* (Altwegg et al. 2005) and around 80% for the colubrid *Drymarchon couperi* (Hyslop et al. 2012).

Unfortunately, comparisons across phylogenetic lineages are hampered by high levels of variation within a single population. An extensive literature on the ecology of snakes has documented very high flexibility in critical life history traits. For example, weather-driven shifts in prey availability can massively modify not only rates of survival, but also of growth and reproduction, and age at maturation (e.g. Madsen and Shine 2000; Brown and Shine 2007; Ujvari et al. 2010). Strong temporal shifts (declines) in the abundance of sea snakes (e.g. Lukoschek et al. 2013)

suggest that rates of survival are similarly variable in marine reptiles. In keeping with that inference, annual rates of survival estimated from our own study varied strongly among years (42–94%: see Table 2). That high level of variation of survival rates through space and time means that current data on survival (and perhaps other life history traits) do not allow robust overall comparisons between terrestrial and marine snakes.

Nonetheless, the high levels of variation in survival rates through space and time, as well as substantial interspecific (and in some cases, intraspecific: Lemen and Voris 1981) variation in traits such as fecundity and frequency of reproduction, are likely to engender corresponding variation in the vulnerability of sea snake populations to threatening processes such as pollution, predation, over-exploitation and coral bleaching. As a result, managers have only limited ability to predict which taxa are most likely to be at risk. The recent expansion of fundamental research into the biology of sea snakes is encouraging, but major knowledge gaps remain (see Udyawer et al. 2018). Until we know far more about these mysterious marine organisms, we are poorly placed to predict and mitigate the impacts of anthropogenic modifications to oceanic environments.

Compliance with ethical standards

Conflict of interest All authors declare no competing interests.

Ethical approval All procedures with live animals conformed to international guidelines for animal welfare and were approved by the University of Sydney Animal Care and Ethics Committee (approval # L04/6-2005/3/4111). Our research was also approved by the relevant wildlife management authority in the Southern Province of New Caledonia (permit 34756-2019-3REP/DENV).

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