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Author for correspondence:
Harvey B. Lillywhite
e-mail: hblill@ufl.edu

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Pelagic sea snakes dehydrate at sea

Harvey B. Lillywhite[1], Coleman M. Sheehy III[1], François Brischoux[2] and Alana Grech[3]

[1]Department of Biology, University of Florida, Gainesville, FL 92611-8525, USA
[2]CEBC UMR 7372 CNRS-ULR, 79360 Villiers en Bois, France
[3]Department of Environment and Geography, Macquarie University, New South Wales 2109, Australia

Secondarily marine vertebrates are thought to live independently of fresh water. Here, we demonstrate a paradigm shift for the widely distributed pelagic sea snake, *Hydrophis* (*Pelamis*) *platurus*, which dehydrates at sea and spends a significant part of its life in a dehydrated state corresponding to seasonal drought. Snakes that are captured following prolonged periods without rainfall have lower body water content, lower body condition and increased tendencies to drink fresh water than do snakes that are captured following seasonal periods of high rainfall. These animals do not drink seawater and must rehydrate by drinking from a freshwater lens that forms on the ocean surface during heavy precipitation. The new data based on field studies indicate unequivocally that this marine vertebrate dehydrates at sea where individuals may live in a dehydrated state for possibly six to seven months at a time. This information provides new insights for understanding water requirements of sea snakes, reasons for recent declines and extinctions of sea snakes and more accurate prediction for how changing patterns of precipitation might affect these and other secondarily marine vertebrates living in tropical oceans.

1. Introduction

Water is essential to life, and it is a key resource especially in dehydrating environments such as deserts and ocean. The Earth's oceans teem with life, yet these salty environments are physiologically challenging because of the virtual absence of fresh water. The evolutionary transition of animals from land or fresh water to a marine habitat therefore is difficult because of the osmoregulatory challenges posed by salinity [1,2]. The successful clades of marine vertebrates that have undergone significant radiations in marine environments—bony fishes, cetaceans, pinnipeds, sea turtles, sea snakes and some birds—are thought to live independently of fresh water and to have overcome the osmoregulatory challenges by evolving anatomical and physiological specializations that maintain water balance (e.g. salt glands in birds and non-avian reptiles) [3]. However, the efficacy of such mechanisms has been questioned recently by noting dependence on fresh water that appears to limit the distribution and abundance of marine snakes [1,4–7].

The yellow-bellied sea snake, *Hydrophis* (*Pelamis*) *platurus*, is the only pelagic species of sea snake and is arguably one of the more marine-adapted species. It is the only sea snake that occurs in the eastern Pacific and, in fact, has the broadest global distribution of any species of squamate reptile. It ranges from coastal southeast Africa across the Indo-Pacific to the shores of Central America where the latitudinal distribution includes the Gulf of California to the north and Ecuador to the south [8].

We have investigated dehydration and drinking behaviour of *H. platurus* since 2009, with special focus on the population of snakes inhabiting the Golfo de Papagayo of northwestern Guanacaste, Costa Rica [4,9–11]. These marine waters and the adjoining dry forest experience drought for roughly half of the year (December through May or June) when rainfall is absent or negligible [12,13] (figure 1). Because *H. platurus* is pelagic and inhabits the open ocean, the only potential source of fresh water in its environment is a brackish

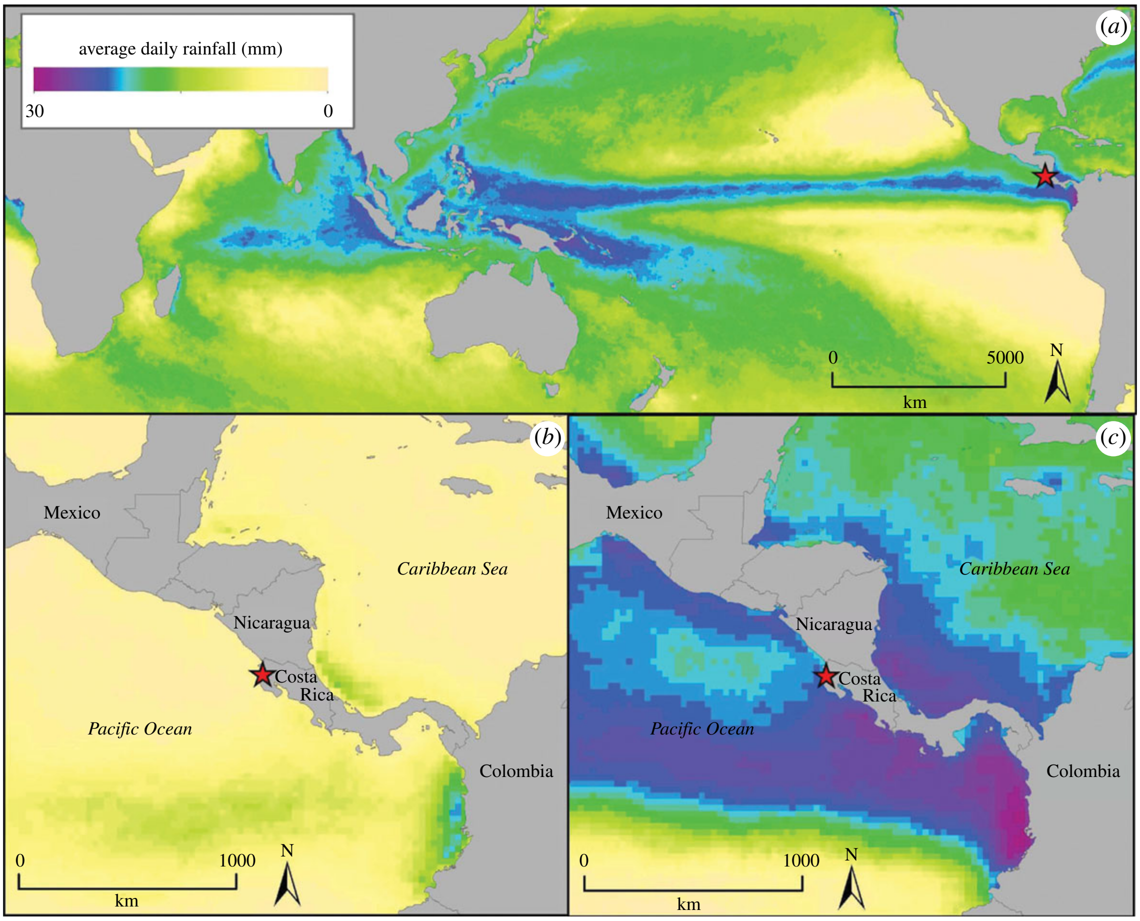

Figure 1. Spatial and temporal patterns of precipitation during the years 2010–2012. (*a*) Daily average rainfall for the tropical Indo-Pacific during the years 2010–2012. (*b*) Daily average rainfall during the dry season, December–May, 2010–2012. (*c*) Daily average rainfall during the wet season, June–November, 2010–2012. Data are from NASA metadata project TRMM v. 7, multisatellite precipitation. Red star represents Golfo de Papagayo, Costa Rica.

or freshwater lens that forms during heavy rainfall and, ideally, minimal mixing conditions of ocean water. Rainfall is more likely to occur over land, so the open ocean can be a virtual 'desert' especially during the dry season (figure 1*b*). Thus, we became interested to test whether this pelagic vertebrate dehydrates at sea. Here, we show that this pelagic species likely spends much of its life in a dehydrated state corresponding to cycles of prolonged seasonal drought.

2. Material and methods

We have made 10 field trips to the Guanacaste coast where, in different seasons, we collected a total of more than 500 live *H. platurus*. We sampled snakes during five to eight consecutive mornings each trip and tested whether they would drink fresh water immediately following capture. Snakes were captured using a dip net, returned to the laboratory in damp mesh bags, weighed to the nearest 0.1 g, placed in fresh water, observed for drinking and finally re-weighed the following morning *ca* 20 h later. Before each weighing to determine mass of a snake, it was gently blotted and allowed to air-dry on a towel for several minutes so the skin surface was dry to the touch and did not hold superficial water. Details and discussion of these methods may be found in previous publications [4,5,14]. Drinking is stimulated by thirst, which in turn indicates some level of dehydration prior to capture [5].

We measured the mass and length of snakes and calculated an index of body condition at capture. The body condition index (BCI) was quantified using residual scores based on linear regression of body size and body mass (log-transformed for linearity) [15,16]. We excluded snakes from analysis if they were gravid with advanced embryos or had fish in the stomach, conditions that we determined by gentle palpation (and in some cases voluntary regurgitation of fish).

We determined the total body water (TBW) of 40 snakes we collected during three of the field sessions in Costa Rica and dried to total desiccation in a 70°C oven. Seven of these snakes appeared as healthy as the others but died of unknown causes at various times following the initial mass determination. The others were euthanized prior to drying in the oven. Two sets of measurements were made at the end of the dry season ($n = 9$, 11), while the other set was obtained at the end of the wet season ($n = 20$).

3. Results

The percentage of snakes drinking varied from 0 to 46% and exhibited a seasonal pattern, with most snakes drinking following periods of low rainfall (figure 2). The BCI was significantly lower in snakes that drank fresh water compared with those that did not drink following their capture (figure 3*a*). Moreover, the amount of water that snakes drank varied inversely with the BCI (figure 3*b*).

Using log-transformed data, mean TBW ($\pm$s.e.) in snakes captured at the end of the dry season (75.2 $\pm$ 0.3% body mass) was significantly lower than that measured in snakes at the end of the wet season (77.7 $\pm$ 0.6% body mass; *t*-test, $p = 0.0005$). In six snakes drinking fresh water, mean TBW was significantly lower before drinking (75.8 $\pm$ 0.9% body

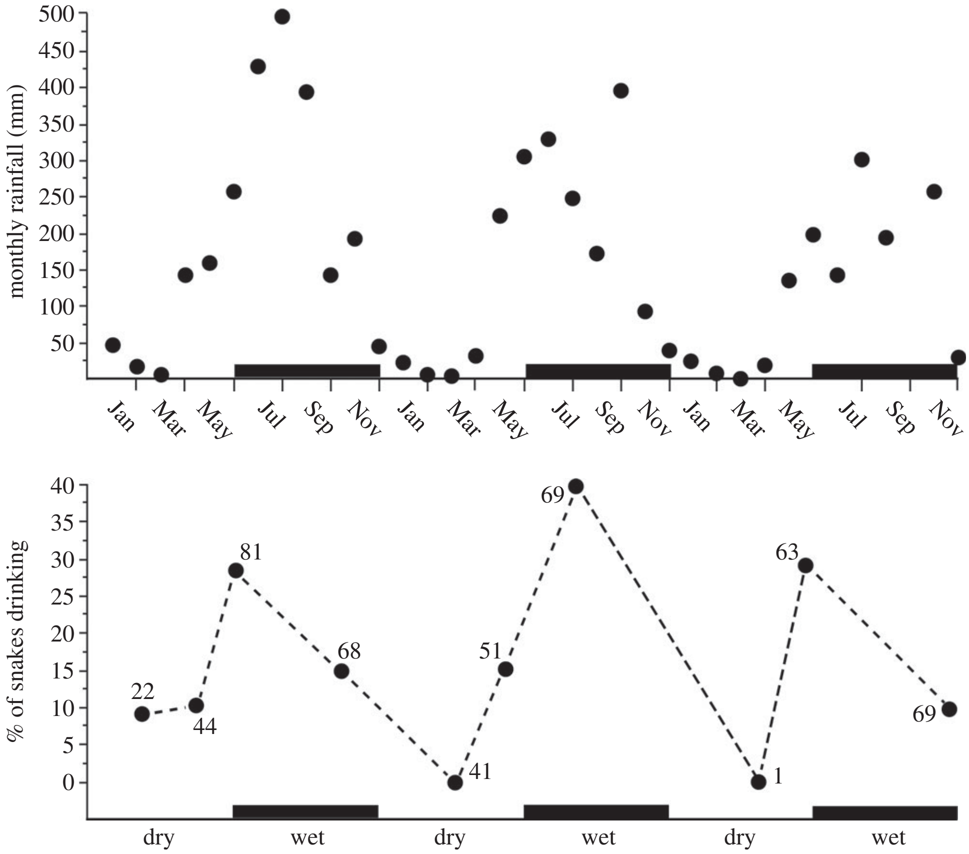

Figure 2. Patterns of monthly rainfall and the percentages of sea snakes (*H. platurus*) drinking fresh water (FW) during three drought cycles at Golfo de Papagayo, Costa Rica. Plots for rainfall are monthly totals, and the snakes drinking are percentages of the snakes sampled ($n =$ numbers next to data points) that drank FW immediately following capture from the open sea. Note that FW drinking increases following periods of several months without significant rainfall. FW drinking decreases following periods having large amounts of precipitation (see text for further explanation of the patterns). Data for rainfall are from NASA, TRMM 3B43 v. 7, and reflect monthly totals for a 25×25 km quadrat of ocean centred at the area from which snakes were collected. The data point representing a single snake (right-hand 'dry season') is included for completeness, although unusual conditions of a red tide combined with cold water, turbidity and high winds prevented a larger sampling of snakes at that time.

mass) than after drinking ($78.6 \pm 1.1\%$ body mass; paired *t*-test, $p = 0.0214$). The maximum TBW we measured varied from 79 to 81.6% in six individuals, and the minimum TBW we measured ranged from 73.3 to 75% in seven individuals.

4. Discussion

Previous studies have demonstrated thirst and drinking—hence dehydration—in amphibious sea kraits that spend time in terrestrial environments ([5,11] and references therein). Here, we show that pelagic sea snakes dehydrate at sea during seasonal drought. While there is an obvious seasonal pattern to drinking, both the numbers of snakes drinking and the seasonal timing of maxima and minima are variable and somewhat offset from the associated pattern of rainfall (figure 2). The observed pattern can be attributable to at least four factors. First, there is variability in the dehydration threshold at which snakes are stimulated to drink fresh water, the mean being a deficit of $-18.3 \pm 1.1\%$ s.e. loss of body mass [4]. Moreover, individuals dehydrated in the laboratory exhibit a range of such deficits spanning from 10 to 27% loss of body mass [4]. Therefore, snakes are likely to be in variable stages of dehydration and may not drink because of the variation and relative insensitivity of the response (high dehydration threshold; cf. amphibious sea kraits: [5]). Second, sea snakes dehydrate slowly in seawater. *H. platurus* loses $0.54 \pm 0.03\%$ body mass per day in laboratory conditions, reflecting an efflux that is likely to be even smaller when snakes are in natural circumstances at sea [4]. Thus, snakes at Guanacaste are expected not to drink until well into the dry season because it requires several months to reach the dehydration threshold for drinking [4]. Third, precipitation is not necessarily tightly correlated with drinking because storms can be brief and spotty in location. Presumably, large and prolonged rain events with appropriate mixing conditions are required for the production of a freshwater lens that is suitable for drinking. Thus, a given storm might 'water' snakes at a particular location, while other individuals remain in drought perhaps only a few kilometres away. Finally, *H. platurus* are pelagic and subject to large-scale movements that involve drifting with currents [8,9,17,18]. Thus, any given collection of snakes for drinking observations might include individuals from locations having unknown histories of precipitation. Prevailing currents on the Guanacaste coast flow from south to north, so snakes drifting from more southerly and less drought-prone locations could arrive having had more recent access to fresh water than did those that might have been resident at Golfo de Papagayo for longer periods.

The BCI we measured in *H. platurus* was significantly lower in snakes that drank fresh water immediately following capture compared with those that did not drink following their capture (figure 3*a*), and the amount of water that

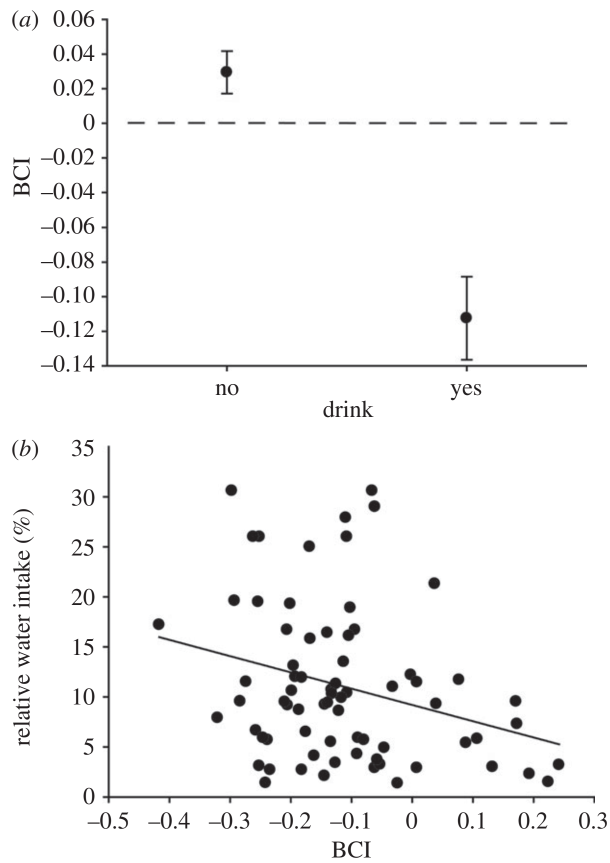

Figure 3. BCI related to consumption of fresh water by sea snakes (*H. platurus*) collected over three wet–dry cycles at Golfo de Papagayo, Costa Rica. Snakes that drink fresh water immediately following capture have significantly lower BCI than do those not drinking (*a*) (ANOVA, log-transformed data, $p \leq 0.0001$), and the amount of water ingested (% original body mass) varies inversely with the BCI (*b*) ($r^2 = 0.067$, $p = 0.0156$).

snakes drank varied inversely with the BCI (figure 3*b*). These results suggest that captured snakes having lower BCI reflect, at least in part, dehydration at sea. Elsewhere, it has been shown that annual increases of oceanic salinity exert a negative effect on BCI in populations of sea snakes inhabiting a lagoon at New Caledonia [6].

The body water content we measured in hydrated *H. platurus* (and some other sea snakes; H.B.L. 2012, unpublished data) is relatively high (roughly 80% body mass in hydrated individuals) compared with that of many other vertebrates, including freshwater snakes (means, 68.6–77.1% body mass [19]) and marine turtles (means, 64–66% body mass [20]). The condition of TBW in sea snakes possibly represents a specialization that enhances dehydration tolerance, or may simply reflect a characteristically lower content of body fat compared with other species [20]. In any event, the extent of dehydration we have quantified in terms of reduced TBW (minima = 73.3–75% in seven individuals) corresponds very well with the expected reductions of TBW if snakes dehydrate to the mean threshold for drinking. A hypothetical loss of 18% body mass owing to dehydration [4] reduces TBW from 80 to 75.6% body mass. The previous measurements of TBW in this species by Dunson & Robinson (73.9% [21]) appear to represent dehydrated animals ($n = 6$).

In summary, data for spontaneous and voluntary drinking of fresh water, as well as the status of hydration and body condition, indicate unequivocally that this species of broadly distributed and exclusively marine snake dehydrates at sea and potentially remains in negative water balance for six to seven months at a time. We also conclude that such dehydration is not effectively mitigated either by functioning of salt glands or the consumption of marine fish [11,14]. Without a source of fresh water, *H. platurus* is in negative water balance in seawater and has sodium turnover rates that are too low to reflect significant ingestion of seawater [21]. Dehydration at sea by this and other sea snakes is quite possibly unique among secondarily marine vertebrates [22,23], and this phenomenon is an important consideration for determining the reasons for recent extinctions and population declines of marine snakes [24]. A more complete understanding of the water requirements in sea snakes and other secondarily marine vertebrates will potentially aid in more accurately predicting how changing precipitation patterns in the tropical oceans might impact these animals [25–27].

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References

1. Brischoux F, Tingley R, Shine R, Lillywhite HB. 2012 Salinity influences the distribution of marine snakes: implications for evolutionary transitions to marine life. *Ecography* **35**, 994–1003. (doi:10.1111/j.1600-0587.2012.07717.x)
2. Dunson WA, Mazzotti FJ. 1989 Salinity as a limiting factor in the distribution of reptiles in Florida Bay: a theory for the estuarine origin of marine snakes and turtles. *Bull. Mar. Sci.* **44**, 229–244.
3. Randall D, Burggren W, French K. 2002 *Eckert animal physiology: mechanisms and adaptations*. New York, NY: WH. Freeman and Co.
4. Lillywhite HB, Brischoux F, Sheehy III CM, Pfaller JB. 2012 Dehydration and drinking responses in a pelagic sea snake. *Integr. Comp. Biol.* **52**, 227–234. (doi:10.1093/icb/ics039)
5. Lillywhite HB, Babonis LS, Sheehy III CM, Tu M-C. 2008 Sea snakes (*Laticauda* spp.) require fresh drinking water: implication for the distribution and persistence of populations. *Physiol. Biochem. Zool.* **81**, 785–796. (doi:10.1086/588306)
6. Brischoux F, Rolland V, Bonnet X, Caillaud M, Shine R. 2012 Effects of oceanic salinity on body condition in sea snakes. *Integr. Comp. Biol.* **52**, 235–244. (doi:10.1093/icb/ics081)
7. Lillywhite HB, Tu M-C. 2011 Abundance of sea kraits correlates with precipitation. *PLoS ONE* **6**, e28556. (doi:10.1371/journal.pone.00228556)
8. Heatwole H. 1999 *Sea snakes*, 2nd edn. Sydney, Australia: University of New South Wales Press.
9. Sheehy III CM, Solórzano A, Pfaller JB, Lillywhite HB. 2012 Preliminary insights into the phylogeography of

the yellow-bellied sea snake, *Pelamis platurus*. *Integr. Comp. Biol.* **52**, 321–330. (doi:10.1093/icb/ics088)

10. Brischoux F, Lillywhite HB. 2011 Light- and flotsam-dependent 'float-and-wait' foraging by pelagic sea snakes (*Pelamis platurus*). *Mar. Biol.* **158**, 2343–2347. (doi:10.1007/s00227-011-1738z)
11. Lillywhite HB. 2014 A desert in the sea: water relations of marine snakes. In *Reptiles in research: investigations of ecology, physiology, and behavior from desert to sea* (ed. W Lutterschmidt), pp. 485–500. New York, NY: Nova Science Publishers.
12. Scott N. 1966 *Ecologically important aspects of the climates of Costa Rica*. San Jose, Costa Rica: Mimeo, Organization for Tropical Studies, Ciudad Universitaria, Costa Rica.
13. Rockwood LL. 1975 The effects of seasonality on foraging in two species of leaf-cutting ants (*Atta*) in Guanacaste Province, Costa Rica. *Biotropica* **7**, 176–193. (doi:10.2307/2989622)
14. Lillywhite HB, Sheehy III CM, Heatwole H. 2014 Dehydration and drinking behavior of the marine file snake, *Acrochordus granulatus*. *Physiol. Biochem. Zool.* **87**, 46–55. (doi:10.1086/673375)
15. Bonnet X, Naulleau G. 1995 Estimation of body reserves in living snakes using a body condition index. In *Scientia herpetologica* (eds G Llorente, X Santos, MA Carretero), pp. 237–240. Barcelona, Spain: Association of Herpetologists Española.
16. Jayne BC, Bennett AF. 1990 Selection on locomotor performance capacity in a natural population of garter snakes. *Evolution* **44**, 1204–1229. (doi:10.2307/2409283)
17. Kropach C. 1975 The yellow-bellied sea snake, *Pelamis*, in the eastern Pacific. In *The biology of sea snakes* (ed. WA Dunson), pp. 185–213. Baltimore, MD: University Park Press.
18. Minton SA. 1975 Geographic distribution of sea snakes. In *The biology of sea snakes* (ed. WA Dunson), pp. 21–31. Baltimore, MD: University Park Press.
19. Dunson WA. 1980 The relation of sodium and water balance to survival in sea water of estuarine and freshwater races of the snakes *Nerodia fasciata*, *N. sipedon*, and *N. valida*. *Copeia* **1980**, 268–280. (doi:10.2307/1444004)
20. Thorson TB. 1968 Body fluid partitioning in Reptilia. *Copeia* **1968**, 592–601. (doi:10.2307/1442030)
21. Dunson WA, Robinson GD. 1976 Sea snake skin: permeable to water but not to sodium. *J. Comp. Physiol.* **108**, 303–311. (doi:10.1007/BF00691678)
22. Ortiz RM. 2001 Osmoregulation in marine mammals. *J. Exp. Biol.* **204**, 1831–1844.
23. Reina RD, Jones TT, Spotila JR. 2002 Salt and water regulation by the leatherback sea turtle *Dermochelys coriacea*. *J. Exp. Biol.* **205**, 1853–1860.
24. Lukoschek V, Beger M, Ceccarelli D, Richards Z, Pratchett M. 2013 Enigmatic declines of Australia's sea snakes from a biodiversity hotspot. *Biol. Conserv.* **166**, 191–202. (doi:10.1016/j.biocon.2013.07.004)
25. Hulme M, Osborn TJ, Johns TC. 1998 Precipitation sensitivity to global warming: comparison of observations with HadCM2 simulations. *Geophys. Res. Lett.* **25**, 3379–3382. (doi:10.1029/98GL02562)
26. Neelin J, Münnich M, Su H, Meyerson JE, Holloway CE. 2006 Tropical drying trends in global warming models and observations. *Proc. Natl Acad. Sci. USA* **103**, 6110–6115. (doi:10.1073/pnas.0601798103)
27. Christensen HJ *et al*. 2007 Contribution of working group I to the fourth assessment report on the intergovernmental panel on climate change. In *Climate change 2007: the physical science basis* (eds S Solomon, D Qin, M Manning, Z Chen, M Marquis, KB Averyt, M Tignor, HL Miller), pp. 848–940. Cambridge, UK: Cambridge University Press.