Physiological, ecological, and behavioural correlates of the size of the geographic ranges of sea kraits (*Laticauda*; Elapidae, Serpentes): a critique

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ABSTRACT

Recent, more accurate delineation of the distributions of sea kraits and prior dubious use of proxy temperatures and mean values in correlative studies, requires re-assessment of the relationships of temperature and salinity as determinants of the size of the geographic ranges of sea kraits. Correcting the sizes of geographic ranges resolved the paradox of lack of correspondence of size of range with degree of terrestriality, but did not form a definitive test of the theory. Recent ecological, physiological, and behavioural studies provide an example of the kind of approach likely to either validate or refute present theory.

1. Introduction

Sea kraits (genus *Laticauda*) and the “true” sea snakes represent separate marine radiations from terrestrial snakes (Sanders et al., 2008; Pyron et al., 2013; Elfes et al., 2013; Lee et al. in press). The “true” sea snakes are viviparous and never

voluntarily leave the sea. Sea kraits differ by being oviparous and amphibious. They come onto land to mate, oviposit, rest, slough their skin, and digest meals. They forage in the sea for their prey of fish, especially eels.

There are three species-complexes within the genus, each with one species distributed widely within the southeastern Asian region and the southwestern Pacific islands, and one or more species with very small ranges within that area (Heatwole *et al.* 2005; (Fig 1). These complexes are: (1) the *Laticauda colubrina* complex with *Laticauda colubrina* being widespread and *Laticauda guineai*, *Laticauda frontalis*, and *Laticauda saintgironsi*, having limited distributions in southern Papua-New Guinea, Vanuatu, and New Caledonia, respectively; (2) the *Laticauda laticaudata* complex with *Laticauda laticaudata* widely distributed and *Laticauda crockeri* restricted to Lake Te-nggano on Rennell Island, Solomon Islands; and (3) the *Laticauda semifasciata* complex with *Laticauda semifasciata*, widely distributed and *Laticauda schistorhyncha* found at Niue Island (Fig. 1).

Species of sea kraits differ in the degree of apportionment of their marine versus terrestrial activities. *Laticauda laticaudata*, and especially *L. semifasciata*, are the more marine and rarely venture far inland, while *L. colubrina* and *L. saintgironsi* are more terrestrial, are adept at terrestrial locomotion, can climb, and frequently occur in the interior of small islands (Shine *et al.*, 2003; Bonnet *et al.*, 2005; Lane and Shine, 2011; Brischoux *et al.* (2013).

The natural history of sea kraits has been summarized by Shine (1991), Heatwole and Guinea (1993), Greer (1997), Ineich and Laboute (2002), Brischoux and Bonnet (2009), and Heatwole (2010). Sea kraits have featured prominently in recent investigations of the physiology, behaviour, and ecology of marine snakes (reviewed in a symposium on sea snakes, see Lillywhite and Brischoux, 2012).

62 Brischoux et al. (2013) investigated how differences in behavioural and
 63 physiological responses to temperature, salinity, and the extent of use of terrestrial
 64 habitats interacted in determining the relative sizes of the distributional ranges of
 65 the three widely distributed species of sea kraits. Using physiological data from
 66 Lillywhite et al. (2009), they reported *L. colubrina* to have the highest rates of
 67 dehydration in sea water and accordingly to occupy seas with low mean salinities,
 68 but conversely to have the lowest rates of transcutaneous evaporative water loss in
 69 air and to occupy the warmest habitat (Table 1). They noted *L. semifasciata* to
 70 have the lowest rates of dehydration in sea water, occupy the most saline habitat,
 71 suffer the highest transcutaneous evaporative loss of water in air, and live in the
 72 coolest habitats. *Laticauda laticaudata* was considered intermediate between the
 73 above two species in all these attributes. Their order of size of geographic ranges
 74 were: *L. laticaudata* largest, *L. colubrina* intermediate, and *L. semifasciata*
 75 smallest (Table 1). There are several sources of difficulty in interpreting the paper
 76 by Brishoux et al. (2013) and the present critique addresses those.

78 **2. A Statistical Problem**

80 Brischoux *et al.* (2013) recognized that their study was based on statistical
 81 correlation without direct evidence of causation and offered the caveat that the
 82 actual mechanism may differ from the one postulated. This is a common problem
 83 for studies based on correlation rather than on more direct, mechanistic
 84 approaches. It is generally recognized that the former approach is more involved
 85 in the generation of hypotheses rather than in testing them, and thus, is not a
 86 serious objection to their study.

3. Use of Mean Values of Environmental Variables

The important statistic is not the mean condition, but the extremes. If the highest, or the lowest, temperatures extend beyond the favourable limits of a species, even for part of the year, it is not relevant that the mean falls within its comfort zone. An example is *L. colubrina* that has breeding populations around part of the perimeter of Taiwan, but not on that part of the coast where a tongue of cold water protrudes seasonally into the strait between Taiwan and mainland China (Heatwole et al., 2012). If means of temperatures are used, one way of somewhat reducing their generality is to portray different times of year separately, rather than using annual means (see Heatwole et al. 2012). This allows detection of areas that have seasonally unsuitable temperatures.

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4. Exclusion of Species with Very Small Ranges

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As indicated above, each complex in the genus has one or more species that have exceedingly small geographic ranges. To validate the theory of Brischoux et al. (2013), these species also need to fit into the postulated model, or it needs to be shown why they are exceptions. Each of these species is closely related to, and derived from, one of the widespread species. Their small ranges could either reflect a loss of the adaptive capacity to deal with temperature or salinity, which seems unlikely, or that factors other than those postulated by the theory are operative. Detailed study of these geographically restricted species are important for assessing the generality of the theory of Brischoux et al. (2013).

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5. Use of Proxy Temperatures

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115 A methodological problem stems from the use of surface temperatures of
 116 the sea as a proxy for land temperatures and relating those to transcutaneous
 117 evaporative losses of water from the snakes. Temperatures of the sea and adjacent
 118 land often are quite disparate and the relationship reverses between day and night
 119 (Foken and Nappo, 2008). Bonnet et al. (2009) noted that at Signal Island, New
 120 Caledonia, the thermal conditions varied greatly among the different microhabitats
 121 available to sea kraits. On ground in the open, temperatures fluctuated from lower
 122 than those of sea water at night to highs of 30°C above that of the sea by day. The
 123 extremes of terrestrial temperatures in the open can be well above the lethal limits
 124 for sea kraits, but are ameliorated by selection of suitable cover under beach rocks
 125 or in burrows where the total span of temperature during a diel period can be less
 126 than 5°C and well within the tolerance limits of the snakes. How well sea-surface
 127 temperatures approximate those experienced by the snakes ashore depends on the
 128 microhabitat selected by the snakes and temperatures may be either higher of
 129 lower than those at the surface of the sea. Bonnet *et al.* (2009) noted that on
 130 Signal Island *L. laticaudata* and *L. saintgironsi* used different types of cover and
 131 accordingly had different body temperatures. Thus, different species of sea kraits
 132 may occupy places with the same sea temperature, but because of differences in
 133 habitat selection on land may have different body temperatures and be subject to
 134 different intensities of evaporative water loss.

135 The use of surface temperatures as a proxy even for the thermal conditions
 136 snakes experience at sea ignores the fact that they can be exposed to vertical
 137 gradients in water temperature (Rubinoff et al., 1986; Heatwole et al., 2012). At a
 138 given location where sea kraits occur (Palau), Colin (2000) found that
 139 temperatures vary vertically, hourly, with wind speed, over diel and tidal cycles,

140 from day to day, seasonally, and at any given time from place to place on the reef.

141 Sea kraits forage and rest on the sea-floor (Heatwole et al. 1978) and
 142 accordingly spend little time at the surface of the ocean. In the laboratory, *L.*
 143 *colubrina* voluntarily submerge from just a few minutes to at least 25 minutes,
 144 depending on level of activity (mean = 19 minutes (Heatwole, 1975, 1981). They
 145 interrupt diving only for short bouts of breathing at the surface (mean number of
 146 breaths 2.5-5.3; range 1-8) (Heatwole, 1981). Cook et al. (2015) found that at sea
 147 almost 99% of dives of *L. laticaudata* and *L. saintgironsi* were <30 m deep
 148 (maximum 82.6 m) and that for the latter species the duration of more sustained
 149 dives (“flat-bottomed” dives) was similar between day (11.9 ± 5.7 min; maximum
 150 37.8 min) and night (10.01 ± 4.7 min; maximum 25.5 min), with respective values
 151 for shorter dives (“V-shaped” or “U-shaped” dives) being 4.7 ± 2.7 ; 12.4 min
 152 (day) and 3.5 ± 2.0 ; 9.9 min (night). Ninety percent of the recovery periods at the
 153 surface were <3 minutes, but longer at night than by day; one *L. saintgironsi* spent
 154 21% of the time at the surface, 58% on the bottom, and 21% in ascent or descent.
 155 Thus, snakes were subjected to surface temperatures briefly compared to the
 156 duration of their exposure to subsurface conditions.

157 The snakes studied by Cook et al. (2015) had mean body temperatures in
 158 the water of $29.3 \pm 1.1^{\circ}\text{C}$ (*L. laticaudata*) and $27.4 \pm 1.5^{\circ}\text{C}$ (*L. saintgironsi*).
 159 Respective temperatures on land were $28.9 \pm 0.9^{\circ}\text{C}$ and $26.2 \pm 0.5^{\circ}\text{C}$. Marine
 160 snakes closely track the temperature of their aquatic environment (Graham 1974;
 161 Heatwole, 1981). Hence, the low variation in body temperatures of snakes at sea
 162 on the reefs studied by Cook et al. (2015) probably reflects weak vertical gradients
 163 in sea temperature at that site. The similarity of the snakes’ body temperatures at
 164 sea and ashore in their study, further suggests that sea temperatures were similar to

those at which the snakes thermoregulate when on land (but not necessarily the prevailing temperatures of the land). Such correspondence of body temperatures in the two media cannot be assumed for all localities, however, as steepness of the thermal gradient in the sea varies from place to place so an area with similar surface temperatures could have different temperatures near the bottom where the snakes forage, even in shallow water. Indeed, on coral reefs, vertical changes in temperature sometimes are greater near shore than they are in deeper water farther offshore (Monismith et al., 2006).

6. Use of Erroneous Distributional Maps.

This is the most serious weakness in the paper. The validity of conclusions is constrained by the quality of the data on which they depend. Brischoux et al. (2013) were unaware that the IUCN distributional maps on which they based their analyses were grossly inaccurate and accordingly they inadvertently suffered from one of the pitfalls of mining data. Most published summaries of the ranges of sea kraits portray distributions of breeding populations as greatly different from reality, often merely citing previous works. The Sea Snake Specialist group in their review of the conservation of marine elapid snakes (Elfes et al. 2013) provided only generalized statements about the distributions of the widespread species of sea kraits, e.g., “widespread, locally abundant” and produced maps only for species with small, local distributions (whose ranges were accurate). Many of the corrections of locality for one of the widespread species (*L. colubrina*) were known at the time of publication of the specialists’ review. The senior author of the present paper (HH) accepts responsibility for this lack of detail as he previously had made many of the corrections himself (e.g., Heatwole et al., 2005; Heatwole, 2010) and, as one of the

specialists on the paper by Elfes et al. 2013), should have brought specific attention to those updates. Heatwole and Cogger (2013) have made additional corrections of sea kraits' distributions and Appendix 1 supplies even more recent ones.

There are several ways of pictorially displaying the distributional ranges of taxa. These vary in the precision with which biogeographic data are portrayed. The least precise is to use polygon⁶ geometry to broadly enclose all localities from which the taxon has been recorded. Obviously, not every living individual of a given taxon is considered in making such polygons and clearly there are gaps where suitable habitats or microhabitats are lacking, not only among locations of individuals, but also among scattered populations. For sea kraits, such polygons enclose non-coastal tracts of land not inhabited by the species (interiors of large islands) as well as expanses of ocean only traversed by dispersing waifs. At best, even if erroneous localities and records of waifs are excluded, polygons still include open water between islands and reefs in which the species does not breed. The informative value of such polygons can be improved by using point geometry to identify localities within polygons where breeding populations have been validly documented (Fig. 1). Points indicate known areas where the species occurs, but leaves presence/absence uncertain in the spaces between points (gaps may indicate absence of collecting activity rather than absence of animals). The IUCN Species Survival Commission (2012) provided a valuable service by defining two levels of precision in the methodology of portraying geographic distributions. They defined "extent of occurrence" (EO) as:

"the area contained within the shortest continuous imaginary boundary which can be drawn to

⁶The use of the term "polygon" here is the traditional "dictionary" sense of a two-dimensional figure formed of three or more straight lines, not the more recent technical derivation used in GIS practice to mean "a closed shape defined by a connected sequence of XY coordinate pairs, where the first and last coordinate pair are the same and all other pairs are unique"
<http://support.esri.com/en/knowledgebase/GISDictionary/term/polygon>

encompass all the known, inferred or projected sites of present occurrence of a taxon, excluding cases of vagrancy....This measure may exclude discontinuities or disjunctions within the overall distributions of taxa (e.g., large areas of obviously unsuitable habitat)....Extent of occurrence can often be measured by a minimum convex polygon (the smallest polygon in which no internal angle exceeds 180 degrees and which contains all the sites of occurrence)." IUCN Species Survival Commission (2012), pp. 11-12.

This is a larger area than the "area of occupancy" (AO), which was defined as: "the area within its 'extent of occurrence' which is occupied by a taxon, excluding cases of vagrancy. The measure reflects the fact that a taxon will not usually occur throughout the area of its extent of occurrence, which may contain unsuitable or unoccupied habitats. In some cases---the area of occupancy is the smallest area essential at any stage to the survival of existing populations of a taxon. The size of the area of occupancy will be a function of the scale at which it is measured, and should be at a scale appropriate to relevant biological aspects of the taxon, the nature of threats and the available data.To avoid inconsistencies and bias in assessments caused by estimating area of occupancy at different scales it may be necessary to standardize estimates by applying a scale-correction factor. It is difficult to give strict guidance on how standardization should be done because different types of taxa have different scale-area relationships." IUCN Species Survival Commission (2012), pp. 12-13.

The caution in the definition---that in order to avoid errors the AO should have a scale-correction factor---is especially important for sea kraits. It is important that the grid squares be sufficiently small. Sea kraits are notorious for their patchy distributions and tend to breed on small offshore cays, from which they radiate over the reef to feed. For example, two cays along the southern coast of Biak, Irian Jaya, Indonesia, that were specifically recommended by local fishermen with an intimate knowledge of the area, yielded sea kraits; search of other seemingly similar cays interspersed along that coast yielded none (HH personal observations). This patchy pattern of local distribution also was observed at a number of other localities throughout sea kraits' ranges. These snakes have high philopatry to specific islands (Shetty and Shine, 2000) and even to a particular part of the shore (Brischoux, et al., 2009). Thus, they may occupy traditional sites to the exclusion of other similar habitat in the vicinity.

A serious problem in interpreting the relationship of physiological variables to distributional patterns is the use of environmental data from over the entire EO, which includes areas outside of the actual area of occupancy.

Although Brischoux et al. (2013) did not present distributional maps, they identified the source of their geographic ranges of sea kraits as the IUCN's maps of EO. The latest version available at that time were those of IUCN (2012) and although not stated, were probably the ones they used; the later version shown in Figure 2 (IUCN, 2014a,b,c,d) was identical and did not correct the inaccuracies of earlier versions. IUCN was not explicit in the labeling of those maps and Brischoux *et al.* (2013) interpreted them as of the EO; instead they seem to be maps of the AO, and hence the error was not as large as would have been the case had the EO been used. Nevertheless, even on IUCN's maps of the AO, the error was great and the ranges used for comparison were not accurate (Table 2). Despite the IUCN specifically excluding records of vagrants (waifs) in defining the EO and AO, their maps for sea kraits did not do so, but included not only areas from which only waifs were known, but also extensive areas that have been shown to be extralimital to sea kraits of any species (Heatwole et al. 2005; Heatwole and Cogger 2013) (Fig. 1; Appendix 1). Depending on the species, from 20% to 39% of the area purported to be inhabited by sea kraits (AO) is not part of their breeding range (Table 2). The environmental variables of the sea also were taken from those areas, which means that 20-39% of the temperatures and salinities used in the analyses were from areas outside of the breeding ranges of the species involved.

7. Discussion

The present critique does not dispute that temperature, salinity, and/or degree of terrestriality may determine particular boundaries of sea kraits' distributions, at least on some of their edges and it is likely that the northern extent

276 of their ranges and their exclusion from other specific areas is attributable to low
 277 temperature of the sea (Heatwole et al. 2012). In fact, during the climatic
 278 fluctuations of the Pliocene and Pleistocene, it is likely that peripheral to the more
 279 thermally stable Coral Triangle where sea kraits originated, extensions and
 280 contractions of ranges may have occurred in response to changes in sea
 281 temperatures (see Heatwole, 2010). The hypothesis of Brischoux et al. (2013),
 282 however, seems simplistic as different borders of the range may be limited by
 283 different factors, e.g., lack of suitable habitat (mangroves instead of coral reefs);
 284 lack of predator-free small islands in otherwise suitable marine habitat; scarcity of
 285 suitable prey (some sea kraits prey only on eels); and physical barriers to dispersal
 286 (see Heatwole et al., 2005).

287 Alone, use of erroneous distributional maps means that neither
 288 corroboration nor invalidation of the theory regarding sizes of sea kraits'
 289 geographic ranges has been achieved. Even were correct distributions used,
 290 substituting surface temperatures of the sea as a proxy for land temperatures is
 291 sufficiently tenuous to render the test inconclusive. Although, in general, where
 292 temperatures of the sea are high, those of the land also tend to be high, thermal
 293 differences from land to sea do vary from place to place. Knowledge of that
 294 variability is needed to assess its biological effect. To take an extreme example,
 295 extend the taxonomic coverage to include all amphibious marine reptiles, not
 296 merely sea kraits. The marine iguana of the Galapagos lives on hot, tropical, xeric
 297 islands and dives to feed on marine algae in very cold water. There, surface
 298 temperatures of the sea (11°-23°C) are not even close to being surrogates of the
 299 temperatures on land where the lizards' preferred range is 35°-39°C and the
 300 maximum voluntarily tolerated is 43°C; body temperature drops to at least 25°C

301 while foraging at sea (Bartholomew 1966, Vitousek et al. 2007). Clearly, sea
 302 kraits are not exposed to such low extremes, but the surrogacy between
 303 temperatures of sea and land cannot be assumed even in more equable climes.
 304 Despite these objections, some aspects of the theory of Brischoux et al.
 305 (2013) intuitively seem reasonable. For example, their conclusion that *L.*
 306 *colubrina* was the most terrestrial species and had the lowest evaporative loss of
 307 water (Table 1) was empirically based. They suggested that this species would
 308 therefore be able acquire fresh water on land better than would *L. semifasciata*, the
 309 most susceptible to desiccation in air, and the least terrestrial in habits. Such is
 310 likely, as resistance to desiccation would allow *L. colubrina* more time for foraging
 311 for sources of water, as would its terrestrial proclivities. The conclusion that this
 312 would lead to *L. colubrina* having a larger distributional range than *L.*
 313 *semifasciata* is less supportable for two reasons. (1) The validity of this
 314 suggestion would depend on the distribution of islands with easy access to fresh
 315 water as opposed to difficult or more remote access, and the degree of aridity of
 316 those islands. If all potential islands had abundant and seasonally consistent
 317 rainfall, such that even *L. semifasciata* would have ready access to fresh water
 318 close to shore at all times, then size of range might not be affected by the relative
 319 susceptibility to evaporative loss in these two species. Critical data would be
 320 whether the islands inhabited by *L. semifasciata* had the above attributes, and
 321 whether *L. colubrina* additionally occurs on islands that either are drier, only have
 322 sources of fresh water remote from the sea's edge, or on which rainfall is
 323 interspersed with long periods of drought.
 324 Brischoux et al. (2012b, 2013; see Lillywhite et al., 2009) empirically
 325 determined that *L. colubrina* dehydrated more quickly in sea water than did *L.*

326 *semifasciata* and consequently, *ceteris paribus*, the latter should be able to survive
 327 oceanic salinities longer than the former. Thus, it should also be expected to
 328 disperse greater distances and thus have a larger distributional range than would
 329 be true for *L. colubrina*. The analysis by Brischoux et al. (2013) placed *L.*
 330 *laticaudata* as intermediate between *L. colubrina* and *L. semifasciata* in all
 331 attributes except size of distributional range (*L. laticaudata* was listed as having
 332 the largest range). The explanation given was that *L. laticaudata* being
 333 “moderately efficient at accessing fresh water on land (Bonnet and Brischoux,
 334 2008), but also moderately resistant to dehydration at sea, occupies the widest
 335 geographic range.” This paradox was resolved, however, by the discovery that the
 336 range of *L. laticaudata* was, in fact, not the largest range of the three widespread
 337 species, but rather the intermediate one (Table 2; Appendix 1) (Gherghel et al.
 338 2016) and therefore more consistent with its physiological attributes.

339 There is a caveat that must be added to any discussion of the the effect of
 340 loss of water from the body. The critical factor in dispersal by sea, or survival
 341 under desiccating conditions, may not only be the rate at which water is lost, but
 342 also the tolerance to water loss (vital limit: percent of the fully hydrated weight
 343 lost as water before death occurs). Other marine snakes have extraordinary
 344 tolerances to loss of body water (Lillywhite et al. 2012, 2014b, 2015). Lillywhite
 345 et al. (2015) recorded water losses of 12-40% (means 27-30%) of hydrated weight
 346 in several species of true sea snakes before they would even drink fresh water
 347 (threshold for drinking) and in the wild some species survived up to seven months,
 348 presumably without access to fresh water. For ethical reasons, desiccation was
 349 not continued to the vital limit, so it is unknown whether there are interspecific
 350 differences in tolerance limits. However, the possibility remains that tolerance

351 may vary among species and one must be aware that a species that loses water
 352 somewhat faster than another species may still survive longer because its
 353 tolerances to loss are greater. Conceivably, rate of loss and tolerance limits could
 354 be independent avenues of adaptation to desiccating conditions.

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356 **8. Prognosis for the Future**

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358 Distributions are not static; they are dynamic and change as barriers to
 359 dispersal are imposed or removed, as waif dispersal and/or migration leads to invasion
 360 of new areas and novel environments, and as the structure of assemblages change
 361 through species being lost via extinction or through adaptation to new combinations
 362 of competitors and predators. The Earth is now in a period of rapid change and the
 363 vicissitudes of a new dynamic, both in the physical environment and in the biotic
 364 *milieu*, doubtless this will lead to adjustments of geographic distributions. There are
 365 many examples of marine fish being caught well beyond their previously known
 366 ranges, especially during El Niño years (NOAA 2016). It is important to know
 367 whether marine snakes and other organisms are responding in a similar fashion. For
 368 example, is the recent finding of seemingly breeding populations in areas peripheral
 369 to previously known distributions (e.g., Wallis et Futuna or South Korea; see
 370 Appendix 1), merely because these species were overlooked previously, or are ranges
 371 expanding? For part of the year, South Korea lies on the colder side of the isotherm
 372 of sea temperatures previously delimiting the breeding ranges of marine snakes
 373 generally (Heatwole et al. 2012). In a country with an intensive fishing industry it is
 374 unlikely sea kraits would not have been noticed previously. Is it because sea snakes,
 375 like marine fish, are moving into new areas as seas become warmer?

376 These peripheral populations and the conditions under which they live should be
 377 studied in detail. On one hand, they may reveal adaptations to colder conditions
 378 that are not seen in more central populations. On the other hand, they may permit
 379 assessing the extension of breeding ranges in response to global warming or other
 380 environmental changes.

381 The groundwork has been laid by delimiting present distributions more
 382 accurately. Now, the primary tasks are to (1) refine more precisely the details of
 383 distribution at the periphery of species' ranges, (2) track extensions of range as
 384 they occur and relate them to alterations in the environment, (3) monitor
 385 microclimates (temperature, salinity), amount and seasonal distribution of rainfall,
 386 and availability of fresh water over a range of localities, and (4) conduct detailed
 387 comparative interspecific studies on the physiological/behavioural responses of
 388 peripheral and central populations. Such research is intensive of labour and is
 389 expensive, but is possible, and indeed necessary for assessing the validity of the
 390 hypothesis of Brischoux et al. (2013) for sea kraits, or for other amphibious
 391 marine animals. A start in this direction has already been made. Attention to
 392 global warming and its effect on reefs has led to monitoring of marine
 393 microclimates (e.g., Colin, 2000, Sobel, 2011, 2013) that can be brought to bear
 394 on the issue at hand. Studies of temperature (Bonnet et al., 2009; Cook et al.,
 395 2015), salinity (Babonis et al., 2012; Brischoux et al., 2012a,b; Cheng et al.,
 396 2013), freshwater (Bonnet and Brischoux, 2008; Lillywhite and Tu, 2011;
 397 Lillywhite et al., 2008, 2009, 2014b; Kidera et al., 2013), and energy budgets
 398 (Dabbruzzi et al., 2012; Cook et al., 2015) all form a basis for comparison over
 399 broader geographic and physiological extents.

400

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Table 1. Ranking of the physiological characteristics of the three widespread species of *Laticauda*, the sizes of their distributional ranges (AO), and the purported thermal and saline characteristics of their habitats. Physiological and thermal data and degree of terrestriality from Brischoux et al. (2013), erroneous sizes of ranges from IUCN (2014a-d), and the ranking of correct sizes from Gherghel (2016) and the present paper; these two papers used different methods for calculating distributional ranges and the resulting absolute sizes were different (see Appendix 1), but the ranking by species agree and both disagree with rankings based on the uncorrected IUCN maps; see Appendix for discussion).

ATTRIBUTES	<i>L. colubrina</i>	<i>L. laticaudata</i>	<i>L. semifasciata</i>
Dehydration in sea water	Highest	Intermediate	Lowest
Salinity of their marine habitat	Lowest	Intermediate	Highest
Evaporative loss of water in air	Lowest	Intermediate	Highest
Surrogate temperature of land	Warmest	Intermediate	Coolest
Degree of terrestriality of the species	Highest	Intermediate	Lowest
Erroneous size of geographic range (IUCN)	Intermediate	Largest	Smallest
Actual size of geographic range	Largest	Intermediate	Smallest

Table 2. Actual and erroneously reported areas of occupancy (AO) of the three widespread species of *Laticauda*.

The area (km²) of erroneous reports and actual distributions of *Laticauda colubrina*, *Laticauda laticaudata*, and *Laticauda semifasciata* were calculated by planimetry of the IUCN maps on Figure, using the software ArcGIS 10.2 (Environmental Systems Research Institute) in the projected-coordinate system ‘Asia South Albers Equal Area Conic’.

SPECIES	TOTAL AREA OF OCCUPANCY (KM ²) ACCORDING TO IUCN MAP	ACTUAL AREA OF OCCUPANCY		ERRONEOUS AREA OF OCCUPANCY	
		KM ²	PERCENT OF IUCN	KM ²	PERCENT OF IUCN
<i>Laticauda laticaudata</i>	6,999,842	4,258,029	61	2,741,813	39
<i>Laticauda colubrina</i>	6,369,594	5,129,653	81	1,239,941	20
<i>Laticauda semifasciata</i>	1,141,007	849,928	75	291,079	26

Figure 1

Figure 2

FIGURE LEGENDS

Figure 1. Distribution of the breeding ranges of sea kraits, showing the actual localities (dots) from which valid specimens are known, surrounded by polygons enclosing all valid records. Top: the species of the *Laticauda colubrina* complex and the infraspecific morphological subunits of *Laticauda colubrina*. Center: the species of the *Laticauda laticaudata* complex. Bottom: The species of the *Laticauda semifasciata* complex. See Heatwole et al. (2005), Heatwole and Cogger (2013) and Appendix 1 for explanation of the corrections made. See Heatwole *et al.* (2005) for the localities of the 1,515 specimens on which the distributional maps of the *Laticauda colubrina* complex are based.

Figure 2. Maps of the geographic distributions of the three widespread species of sea kraits, *Laticauda colubrina*, *Laticauda laticaudata*, and *Laticauda semifasciata*, as portrayed by IUCN (2012, 2014a-d). The portions of the distributions believed to be erroneous or unreliable (see Heatwole *et al.* 2005; Heatwole, 2010) are shown in red. *Laticauda semifasciata* has not been studied as well as the other species and whether it is continuously distributed throughout its north-south range, or whether there is a gap between the populations in the Philippines and the Lesser Sunda Islands is not clear. Modified from IUCN maps with the permission of the International Union for the Conservation of Nature.