



Marine lifestyle is associated with higher baseline corticosterone levels in birds

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Because seawater is hyperosmotic relative to body fluids of most vertebrates, marine lifestyle is expected to strongly influence the physiology of marine tetrapods. Regulating the salt content of body fluids is energetically costly; and osmoregulatory organs may not totally overcome salt load and/or water loss. As a consequence, marine lifestyle should influence physiological systems involved in the maintenance of the physiological balance (homeostasis), in the mobilisation of energetic resources (e.g., to fuel salt excretion), or in the acquisition of resources (e.g., fresh water). Corticosterone (CORT) is one such 'generalist' mediator that is linked with energy expenditure, physiological stress and that activates osmoregulation. As a consequence, CORT is expected to be overall higher in marine tetrapods but this hypothesis has never been tested. Using comparative analyses, we tested this hypothesis in birds, a lineage for which available data on baseline CORT allow comparing marine versus terrestrial species, and species with or without salt glands. We found that marine species (and species with salt glands) display significantly higher baseline CORT during the wintering (but not the breeding) stage. Although salt glands' presence was tightly linked to phylogeny, our results suggest that marine lifestyle may impose a strong, but overlooked, influence on the allostasis-related physiology of marine birds. Such habitat-related variation in physiology is a major phenomenon to explore owing to its general implications for understanding the physiological basis of evolutionary transitions in habitat use. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, **115**, 154–161.

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INTRODUCTION

Evolutionary transitions in habitat use provide powerful opportunities to understand how the environment shapes the morphology, physiology or behaviour of organisms (Little, 1990; Mazin & de Buffrénil, 2001). For instance, tetrapods that are adapted to marine life offer examples of such evolutionary

changes in organismal traits (Mazin & de Buffrénil, 2001). Marine life exerts selection on traits such as the ability to move efficiently through water; to remain underwater for long periods without needing to surface to breathe; and to dive to considerable depths (Kooyman, 1989).

Although widely studied, the respiratory physiology of marine tetrapods is not the only target of selective pressures. Other characteristics of the marine environment, notably its chemical properties, are equally expected to strongly influence the physiology of secondarily marine vertebrates. Due to its elevated

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concentration of sodium chloride, seawater is hyperosmotic relative to the body fluids of most vertebrates. As a consequence, these organisms tend to gain salt and/or to lose water across permeable surfaces. Accordingly, to maintain their osmotic balance, marine tetrapods have evolved specific structures that allow them to regulate the salt content of their body fluids (sophisticated nephrons in mammals, salt glands in non-mammalian marine tetrapods [Ortiz, 2001; Babonis & Brischoux, 2012]).

Functional aspects of osmoregulation have been relatively thoroughly studied (Peaker & Linzell, 1975; Skadhauge, 1981; Ortiz, 2001; Bentley, 2002). However, some other facets of osmoregulatory physiology have been mostly overlooked to date. For instance, excreting excess salt necessitates the activation of specific physiological systems and it also requires energy expenditure (Schmidt-Nielsen, 1983). Additionally, specific osmoregulatory organs may not totally overcome salt load and/or water loss and many marine vertebrates may experience frequent and/or prolonged periods of hypernatremia or dehydration (Brischoux *et al.*, 2012, 2013; Brischoux & Kornilev, 2014; Lillywhite *et al.*, 2012, 2014). All of these parameters should strongly influence the overall physiology of marine tetrapods, including systems involved in the maintenance of the physiological balance (homeostasis), in the mobilisation of energetic resources (e.g., to fuel salt excretion), or in the acquisition of resources (e.g., fresh water).

Glucocorticoids (henceforth ‘GC’) are well studied mediators of organismal allostasis, which is the process of restoring homeostasis (i.e. stability) through physiological or behavioural changes (McEwen & Wingfield, 2003; Romero, Dickens & Cyr, 2009; Angelier & Wingfield, 2013). When an environmental change occurs (e.g., stressors, energetic challenges, climatic events), the activation of the hypothalamic–pituitary–adrenal (HPA) axis results in an increase of circulating GC levels; which in turn leads to specific physiological and behavioural adjustments. These adjustments are expected to allow the organisms to cope with potentially challenging situations (Wingfield *et al.*, 1998; Sapolsky, Romero & Munck, 2000; Romero, 2004). GC, and especially corticosterone (hereafter CORT) may equally respond to the aforementioned osmoregulatory physiology of marine life for several reasons. First, excreting excess salt is energetically costly, and CORT is known to be linked with energy expenditures (Astheimer, Buttemer & Wingfield, 1992; Landys, Ramenofsky & Wingfield, 2006; DuRant *et al.*, 2008; Lynn, Prince & Phillips, 2010). Second, CORT, as a ‘stress hormone’, may respond when organisms undergo some form of physiological stress, such as osmotic stress (Allen, Abel & Takemoto, 1975). Finally, corticosteroids are

important mediators of osmoregulation and they are involved in the control of salt and water balance in most vertebrates (reviewed in McCormick & Bradshaw, 2006). For instance, CORT triggers the functioning of salt glands in birds (Allen *et al.*, 1975; Peaker & Linzell, 1975; Skadhauge, 1981; Bentley, 2002), and high CORT levels can be tightly linked with an activation of osmoregulation processes (Harvey & Phillips, 1980; Tome, McNabb & Gwazdauskas, 1985; Arnason *et al.*, 1986).

Taken together, these elements strongly suggest that CORT levels may be higher in marine, compared with terrestrial, tetrapods because of the osmoregulatory physiology. In this study, we tested this hypothesis using a phylogenetic comparative analysis of 101 bird species for which baseline corticosterone levels are available. Birds are well suited to test such hypothesis. First, this lineage contains both terrestrial and marine species. Second, many species of birds, including a large number of terrestrial species, are known to possess salt glands, while other species (passerines, terrestrial only) lack these organs (Babonis & Brischoux, 2012). Finally, birds have attracted strong attention from stress physiologists over the last decades thereby producing the largest dataset of CORT levels available to date (Wingfield, O’Reilly & Astheimer, 1995; Romero, 2002; Bókony *et al.*, 2009; Hau *et al.*, 2010; Lendvai *et al.*, 2013). Specifically, we independently tested two predictions. First, because of the relationship between CORT and parameters linked to osmoregulation (McCormick & Bradshaw, 2006), baseline CORT levels should be higher in marine birds as compared to terrestrial ones. Second, because the functioning of the salt gland is tightly linked to CORT secretion (Allen *et al.*, 1975), baseline CORT levels should be higher in birds possessing salt glands.

MATERIAL AND METHODS

DATA COLLECTION

Baseline CORT levels were extracted from the dataset published in Lendvai *et al.* (2013) and was completed by species for which recent studies had published CORT data (Boyle, Norris & Guglielmo, 2010; Angelier *et al.*, 2013; Schmid *et al.*, 2013). In May 2013, we searched for articles on the ISI Web of Knowledge database using the keyword ‘corticosterone’ and we kept only the studies that were conducted in free-living adult birds. We focused only on baseline CORT levels as they are unaffected by the stress of capture, and therefore, they should be a good proxy of the allostatic state of free-ranging individuals. Indeed, CORT levels are expected to increase as energetic or environmental constraints increase. This

increase mediates physiological and behavioural changes that help the organism to restore a stable allostatic state (McEwen & Wingfield, 2003; Romero *et al.*, 2009; Angelier & Wingfield, 2013). Additionally, the osmoregulatory action of CORT is thought to be mediated through binding to high-affinity receptors, which are associated with baseline CORT levels (Landys *et al.*, 2006). We only included data from studies that measured CORT from blood samples taken immediately after capture within 3 min (Romero & Reed, 2005) or more if the study validated that CORT levels had not begun to increase during that time interval (Bókony *et al.*, 2009). Previous studies have shown that species' baseline CORT levels range over almost two orders of magnitude and are highly repeatable across different studies that sampled different populations or applied different sampling and assay procedures (Bókony *et al.*, 2009; Lendvai *et al.*, 2013). In each sex, we calculated the weighted mean (by sample size), and then we used the mean value of the sexes to generate one baseline value per species. Although sex-specific analyses were not carried out, the reason for collecting sex-specific values was to control for potential bias in sampling in the original studies. Baseline CORT data were divided into two seasons (wintering and breeding), as these different life-history stages have been shown to affect baseline CORT levels (reviewed in Romero, 2002). Baseline CORT values were log-transformed for analyses.

Habitat use was collected from field guides and the authors' personal experience. We produced two straightforward habitat categories: birds were considered as following a marine lifestyle when they used extensively (e.g., to forage) marine environments (such as oceans, seas, brackish or saltwater coastal marshes) and thus were supposedly susceptible to higher salinity. All other species of birds were considered as terrestrial. This latter category includes three species that can be found in arid habitats. Although the low number of such species in our dataset prevented the inclusion of this additional habitat type in our analysis, we emphasize that including them in the terrestrial category is conservative and thus should not generate spurious patterns. Three species which shifted habitats between seasons (*Calidris mauri*, *C. pusilla*, *Histrionicus histrionicus*) were categorized as terrestrial when breeding and marine when wintering as the foraging habitat used by these species strongly differed between seasons. The presence or absence of salt glands was determined based on the review published by Babonis & Brischoux, (2012). Altogether we used data from 101 bird species (Appendix S1).

To control for the effects of potentially confounding variables, we collected data on aspects of interspecific

life-history variation that have been shown to be related to CORT levels. We gathered data on body mass because larger birds have lower baseline CORT levels, indicating a lower overall metabolism and/or that large mass may serve as a buffer against some stressors (Bókony *et al.*, 2009; Hau *et al.*, 2010). We calculated the average of male and female body mass where sex-specific data for body mass were available, and used their average in the analyses. Although sex-specific analyses were not performed, the reason for collecting sex-specific data for body mass was to control for potential sex-biased sampling for some species. Body mass was log-transformed before the analyses. CORT levels may vary latitudinally (Silverin, Arvidsson & Wingfield, 1997; Breuner *et al.*, 2003; Bókony *et al.*, 2009; Hau *et al.*, 2010). Therefore we collected data on the latitude of each study site, then we calculated the mean latitude weighted by the sample size for each species and for each life-history stage. We also collected data for brood value (i.e., value of current reproduction relative to the lifetime reproductive output of a species, Bókony *et al.*, 2009), expressed as $\log_{10}[\text{clutch size}/(\text{clutch size} * \text{broods per year} * \text{average reproductive life span})]$ which may affect baseline CORT (Bókony *et al.*, 2009). However, we did not include this variable in the final analyses for several reasons. First, brood value was available for less than half of the species under focus, thereby substantially decreasing the power of our analyses. Second, variation in brood value is partially captured by body mass in our dataset as shown by the relatively strong correlation between these two variables ($r = -0.66$, $P < 0.001$, $N = 41$). Finally, preliminary analyses have shown that our results remain similar when including brood value (results available from the authors upon request).

STATISTICAL ANALYSES

We investigated relationships between baseline CORT levels and marine/terrestrial lifestyle and the presence of salt glands with Bayesian phylogenetic mixed-effects models based on Markov chain Monte Carlo estimations, as implemented in the R package 'MCMCglmm' version 2.17 (Hadfield, 2010; Hadfield & Nakagawa, 2010; R Core Team, 2013). Shared ancestry was taken into account by specifying a phylogenetic variance-covariance matrix, using a composite tree compiled from recent molecular phylogenies (Bókony *et al.*, 2009; Lendvai *et al.*, 2013). In order to make our conclusions more robust, we used three different backbones for our phylogenetic tree that differ in branching of the major clades: (1) Davis and Page's phylogenetic supertree (Davis & Page, 2014, Appendix S1), (2) Hackett *et al.*'s tree (Hackett *et al.*, 2008, Appendix S1), and (3) the

Sibley-Ahlquist tree (Sibley & Ahlquist, 1990, Appendix S1). For each tree we used the topology from the respective source with branch lengths transformed according to Nee's method (Maddison & Maddison, 2006). We also used a model in which species were treated as independent samples. We compared these models using the Deviance Information Criterion (DIC) (Hadfield, 2010), which is the Bayesian equivalent of the more commonly used Akaike Information Criterion. We report the parameter estimates (posterior means) and corresponding 95% credibility interval (CI) values.

First, we analysed whether marine versus terrestrial lifestyle and the presence of salt glands were related to baseline CORT levels using different assumptions about the evolutionary history of the clades (three different phylogenies and no phylogeny, i.e. species as independent samples). In these initial models we used marine versus terrestrial lifestyle or the presence of salt glands, the season (wintering or

breeding) and their interaction as fixed effects. Then we further investigated whether our results hold when we included body mass and latitude and their interactions with habitat or the presence of salt glands as potential confounding covariates in the analyses.

RESULTS

Models using four different phylogenetic hypotheses received similar support by DIC (Table 1). As the Davis & Page (2014) tree performed slightly better than the rest (Table 1), we report below the models using this phylogeny. Baseline CORT during the breeding season did not differ significantly between species with or without salt glands (Table 2). However, during wintering, species possessing salt glands had significantly higher baseline CORT levels than species lacking salt glands (Table 2, Fig. 1). Similarly, baseline CORT levels did not differ significantly between marine and terrestrial birds during the breeding season (Table 2), but during wintering, marine species had significantly higher baseline CORT than terrestrial species (Table 2, Fig. 2). The three species that shifted from terrestrial to marine habitat between breeding and wintering had all higher baseline CORT in the marine habitat (Fig. 3).

Body mass tended to have a negative effect on baseline CORT levels, although this effect overlapped with zero (-0.045 , 95% CI $[-0.176, 0.085]$). Higher latitude was associated with higher baseline CORT levels, although this effect was small (0.01 , 95% CI: $[0.003, 0.017]$). Accordingly, controlling for body size or latitude did not alter the relationships of baseline CORT levels with habitat and salt glands qualitatively. Although low sample sizes in some categories impeded robust analyses (e.g., terrestrial with salt gland during winter), we found that restricting our analyses to species for which we had data for both seasons, or comparing terrestrial and marine birds

Table 1. Deviance Information Criterion (DIC) for models using different phylogenetic topologies

	Phylogenetic model	DIC	Δ DIC
Salt glands	Davis & Page (2014)	227.5	
	Hackett <i>et al.</i> (2008)	228.2	0.7
	No phylogeny	231.8	4.3
	Sibley & Ahlquist (1990)	232.9	5.4
Habitat	Davis & Page (2014)	226.9	
	Hackett <i>et al.</i> (2008)	228.1	1.2
	No phylogeny	229.3	2.4
	Sibley & Ahlquist (1990)	230.7	3.8

Differences between DIC values (Δ DIC) were small, indicating that models using different topologies gave qualitatively similar results, but the Hackett *et al.*'s (2008) phylogeny received slightly better support for both sets of analyses. See text for details.

Table 2. Parameter estimates, corresponding 95% credibility intervals (CI) and Bayesian *P*-values from the MCMC linear mixed model analysing log-transformed baseline CORT levels in relation to habitat use and salt gland presence

	Effect	Parameter estimate	Lower 95% CI	Upper 95% CI	<i>P</i> -value
Salt Glands	Intercept (terrestrial, breeding)	2.29	1.69	2.97	< 0.001
	Salt gland	-0.13	-1.07	0.66	0.77
	Season (wintering)	-0.56	-0.83	-0.30	< 0.001
	Season \times salt gland	0.78	0.25	1.28	0.004
Habitat	Intercept (terrestrial, breeding)	2.25	1.78	2.72	0.001
	Marine lifestyle	-0.17	-0.64	0.39	0.51
	Season (wintering)	-0.56	-0.81	-0.32	0.001
	Season \times marine lifestyle	1.06	0.48	1.76	0.002

Shared evolutionary ancestry was taken into account by the Davis & Page (2014) phylogeny (see Table 1). Season refers to life-history stage (breeding or wintering). See text for details.

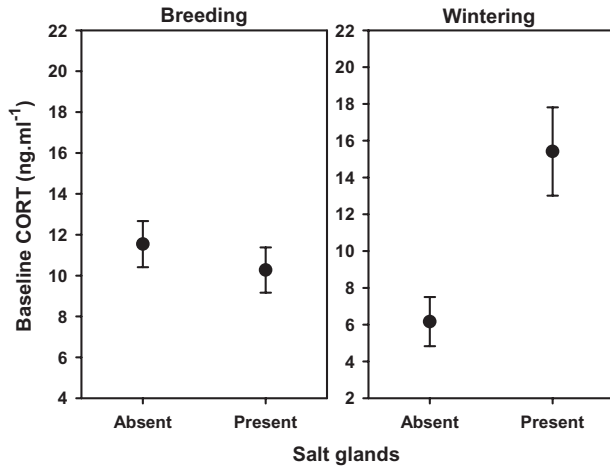


Figure 1. Baseline CORT (simple mean \pm SE) in birds with or without salt glands during the breeding (respectively $N = 46$ and $N = 46$) and the wintering stages (respectively $N = 7$ and $N = 27$). Birds with salt glands display significantly higher baseline CORT during the wintering stage. See text for details. SE, standard error.

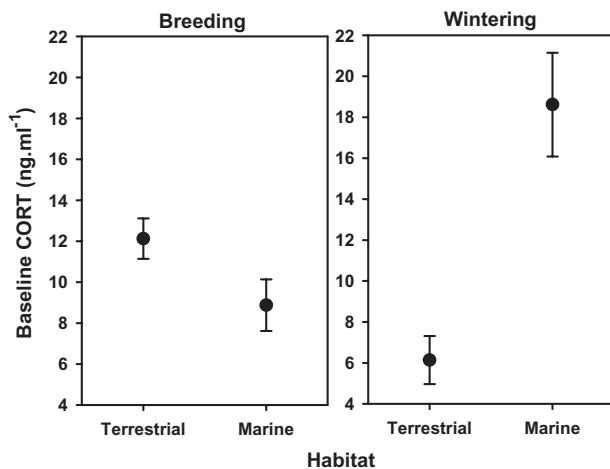


Figure 2. Baseline CORT (simple mean \pm SE) in terrestrial and marine birds during the breeding (respectively $N = 57$ and $N = 35$) and the wintering stages (respectively $N = 28$ and $N = 6$). Marine birds display significantly higher baseline CORT during the wintering stage. See text for details. SE, standard error.

having salt glands, produced qualitatively similar patterns (results available from the authors upon request).

DISCUSSION

Overall, our comparative analyses support the hypothesis that marine lifestyle is linked with higher baseline CORT levels in birds, presumably because of

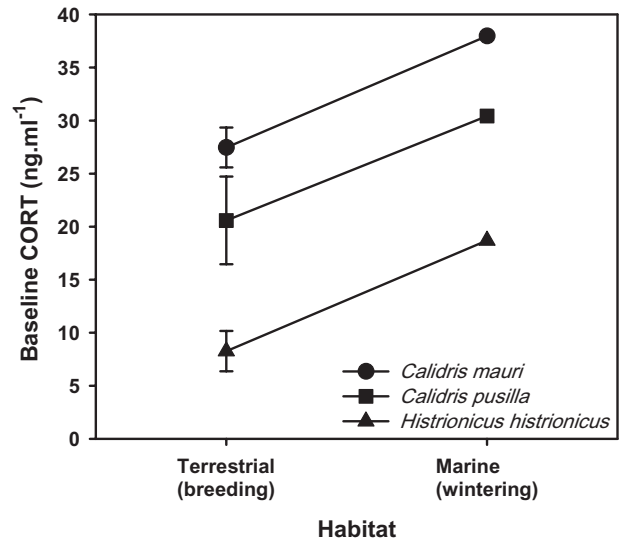


Figure 3. Baseline CORT (simple mean \pm SE) in three species of birds having salt glands (*Calidris mauri*, *C. pusilla*, *Histrionicus histrionicus*) that shift from terrestrial to marine habitat between breeding and wintering. Note that only one value of baseline CORT was available during wintering for these three species. SE, standard error.

the strong osmotic challenge linked to life in seawater. Unexpectedly, we found that the relationship between baseline CORT levels and the habitat (marine versus terrestrial) was only apparent during the non-breeding season, suggesting a strong influence of life-history stage on the relationship between baseline CORT levels and marine life or presence of salt glands. This difference between seasons may be directly linked to the modulation of CORT secretion throughout the life cycle (Romero, 2002; Romero, Cyr & Romero, 2006). Indeed, reproduction is known to produce a significant elevation of baseline CORT levels in birds (Romero, 2002); which is thought to support the energetic demands of the reproductive period. The concomitant increase in energetic demands and baseline CORT levels may mask the influence of other factors. For example, because baseline CORT increases with brood value (Bókony *et al.*, 2009), and because terrestrial birds often have high brood value (e.g. -0.53 ± 0.04 SE in our sample, compared with -0.98 ± 0.05 SE in marine birds), this may influence their baseline levels more than those of marine birds during reproduction; despite the possible influence of osmoregulation on baseline CORT levels in marine species. Alternatively, seasonal variations in CORT levels may follow different patterns depending on habitats. For instance, desert birds tend to show lower CORT during breeding (Romero, 2002). Such example could indicate that seasonal variations

in CORT levels may follow different patterns depending on habitats, and that lower CORT during breeding may be linked to hydric constraints (i.e., deserts and oceans impose similar hydric shortage). Clearly, baseline CORT variations in relation to life-history stage and fresh water availability require specific investigations. In addition, future studies could usefully compare non-breeding and breeding individuals during the reproductive period as it would allow testing whether the positive influence of marine life/salt glands on baseline CORT levels is present during the breeding period in individuals that are not engaged in reproduction.

Among non-breeding birds, we found that marine birds display higher baseline CORT levels than terrestrial birds. Baseline CORT levels were also elevated in species with salt glands. Taken together, these results strongly suggest that CORT secretion and osmoregulation are tightly linked. This functional link was further supported by specific examples. Species that shift from terrestrial to marine habitat between breeding and wintering had significantly higher baseline CORT when using marine habitats, against the overall trend that baseline CORT values were higher during breeding. Supporting our comparative results, intraspecific studies have found that CORT is involved in the process of osmoregulation (Peaker & Linzell, 1975; Skadhauge, 1981; Bentley, 2002; Landys *et al.*, 2006) and also in the functioning of the salt glands (Allen *et al.*, 1975).

There are a few caveats to our study, notably regarding the effects of salt gland on basal CORT levels. Indeed, the salt gland seems to be an ancestral trait in most birds (Babonis & Brischoux, 2012), and it may have been lost during a single evolutionary event sometime during the evolution of Passeriformes (Shoemaker, 1972; Babonis & Brischoux, 2012). As a consequence, for this specific analysis, we cannot robustly tease apart the respective role of phylogeny versus presence/absence of salt glands. Although we acknowledge that this result needs to be interpreted with caution, several elements suggest that our analysis did not generate spurious patterns. First, the fact that CORT levels are higher in birds with salt glands is in line with our *a priori* prediction. Indeed, salt gland functioning is energetically costly, and CORT levels correlate with energy allocation and metabolic rates (Sapolsky *et al.*, 2000; Landys *et al.*, 2006). Detecting a significant positive relationship between salt gland presence and CORT levels was expected, independently of any phylogenetic considerations. Second, none of the other traits that we have included in our analysis (e.g., body mass, latitude) altered our conclusions, while, at least body mass differs extensively between passerine and non-passerine birds. This suggests that the effect of salt glands on baseline

CORT levels should be relatively strong compared to other variables. If this result was a by-product of body size solely, this result would have been similar during the breeding season, because the body mass difference between groups is comparable. On the contrary, baseline CORT levels during reproduction were similar between passerine (lacking salt glands) and non-passerines (with salt glands) birds. This suggests that CORT levels may vary similarly between these two phylogenetically distinct groups, at least during reproduction. Importantly, there was no obvious way for us to remove such bias (e.g., to produce a passerine bird having salt glands). Despite such limitation, we believe that including this result, although putatively fragile, is critical in the context of our study.

The reasons why non-breeding baseline CORT levels are higher in marine birds (or in birds having salt glands) are probably multiple. CORT is a 'generalist' physiological mediator which is involved in functions as diverse as acquisition of resources, mobilization of energy stores and their allocation (Landys *et al.*, 2006; Lynn *et al.*, 2010), metabolic rates (Astheimer *et al.*, 1992; DuRant *et al.*, 2008), movements and activity (Angelier *et al.*, 2007; Crossin *et al.*, 2012), or stress response (Wingfield *et al.*, 1998; Angelier & Wingfield, 2013). In addition, and interestingly in the context of our study, CORT as a mineralocorticoid may also be involved in the maintenance of the osmotic balance (Peaker & Linzell, 1975; Skadhauge, 1981; Bentley, 2002; McCormick & Bradshaw, 2006). All these functions or organismal responses are likely to be influenced by marine lifestyle. For instance, excreting excess salt is energetically costly, and CORT may be higher in marine birds (or in birds having salt glands) because they have higher energetic requirements in order to fuel salt gland functioning (Schmidt-Nielsen, 1983). Similarly, marine species may experience frequent and/or prolonged period of hypernatremia or strong dehydration (i.e., osmotic stress) which may provoke the activation of the HPA axis to produce dedicated physiological and behavioural responses (e.g., to reduce additional water loss, or to acquire fresh water when available). Finally, the higher levels of CORT we detected in marine birds (or in birds having salt glands) may be as a consequence of the role of CORT as a mediator of osmoregulation (Harvey & Phillips, 1980; Tome *et al.*, 1985; Arnason *et al.*, 1986).

Although our study does not allow elucidating the physiological basis of the habitat-related variation in CORT levels we detected, our analyses strongly suggest that marine life is related to a bird's baseline CORT level. Such link is presumably related to the maintenance of the physiological balance (homeostasis), in the mobilisation of energetic resources (e.g., to fuel salt excretion), or in the acquisition of resources

(e.g., fresh water) all of which are required by life in seawater. Ecological and evolutionary impacts of such physiological systems have been largely overlooked in the context of habitat use. Future experimental studies will be critical to disentangle the physiological causes of CORT variation between habitats. More generally, we believe that such habitat-related variation is a major phenomenon to explore owing to its general implications for understanding the physiological basis of evolutionary transitions in habitat use.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher’s web-site:

Appendix S1. Illustration of the three phylogenetic hypotheses analysed in this study. (A) Davis and Page’ phylogenetic supertree (Davis & Page, 2014), (B) Hackett *et al.*’s tree (Hackett *et al.*, 2008) and (C) the Sibley-Ahlquist tree (Sibley & Ahlquist, 1990). Red and black branches illustrate species with or without slat glands, respectively. Blue font represents marine species, green font represents terrestrial species, and brown font indicates species that shift habitats between life-history stages.